BIOCOMPLEXITY OF NONSORTED CIRCLES IN THE LOW ARCTIC, ALASKA

A

Thesis

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

Anja N. Kade, B.S., M.S.

Fairbanks, Alaska

May 2006

BIOCOMPLEXITY OF NONSORTED CIRCLES IN THE LOW ARCTIC, ALASKA

By

Anja N. Kade

RECOMMENDED:

Advisory Committee Chair

Assistant Chair, Department of Biology and Wildlife

APPROVED:

Dean, College of Natural Science and Mathematics

Dean of the Graduate School

April 7, 2006

Date

ABSTRACT

The vegetation and soils in many arctic tundra regions are influenced by the distribution of nonsorted circles, unique patterned-ground features that dot the well-vegetated tundra landscape. They are flat to dome-shaped, bare soil patches 0.5 to 3 m across and lack a border of stones. Localized soil disturbance due to cryogenic processes creates unusual micro-environments with unique plant communities, slow soil development and deep active layers. The contrast between barren nonsorted circles and the well-vegetated stable tundra provides an ideal opportunity to examine the complex linkages among vegetation, soil and disturbance through cryogenic processes, offering insight into how the tundra system operates. The central goal of this thesis is to understand the complex linkages of the nonsorted-circle system along a natural climate gradient on the North Slope in the Alaskan arctic tundra at different scales, ranging from plot level to regional changes.

This thesis examines the interactions among vegetation, soil and cryogenic regime by treating the nonsorted circles within the stable tundra as a single complex system. The thesis presents a formal description and analysis of the plant communities on and off nonsorted circles along the climatic gradient using the Braun-Blanquet classification approach. The thesis also studies the physical effects of vegetation, soil organic mat and snow cover on the microclimate of nonsorted circles and the stable tundra along the same climate gradient. The influence of vegetation on cryogenic processes is examined experimentally by manipulating the plant canopy on nonsorted circles.

When compared to the stable tundra, nonsorted circles have minimal vegetation cover, resulting in warm soil temperatures and deep thaw depths in summer and allowing for increased ice-lens formation during freeze-up. The resulting frost heave and needle-ice formation at the soil surface maintain the bare surfaces of the circles through soil disturbance. Cryogenic processes dominate the system at the northern sites, while the warmer climate towards the south allows for thick vegetation mats on and off the nonsorted circles, suppressing cryogenic processes. The strength of the interactions among vegetation, soil and cryogenic regime may change under a warming arctic climate, possibly leading to the local disappearance of nonsorted circles.

TABLE OF CONTENTS

Page

LIST OF FIGURES

Page

LIST OF TABLES

Page

ACKNOWLEDGEMENTS

I gratefully acknowledge financial support for this research from the NSF Biocomplexity Grant (OPP-0120736), the UAF Center for Global Change Student Grant, the Randy Howenstein Memorial Field Research Scholarship, and the UAF Thesis Completion Fellowship.

I am thankful to my advisor Dr. Donald Walker, who taught me an appreciation for the arctic tundra, never tired of my questions and encouraged me to do high-quality work. My committee members Dr. Christa Mulder, Dr. Chien-Lu Ping and Dr. Vladimir Romanovsky offered excellent input into research design and analysis. The staff at the Alaska Geobotany Center provided good comments on practice talks, help with computer trouble and distraction in the form of lunch-break ski outings.

I would like to thank Erin Cushing, Alexia Kelley and Eamon O'Regan for valuable field assistance and the UAF Palmer Soil and Plant Analysis Laboratory for soil analyses. Dr. Olga Afonina and Dr. Misha Zhurbenko identified the nonvascular plants of my study sites, and Prof. Dr. Fred Daniëls helped with the syntaxonomy of the plant communities.

For all research, I took the lead role in design, implementation and synthesis. Dr. Donald Walker contributed in an advisory capacity and is therefore co-author of all manuscripts. Martha Raynolds helped significantly with the vegetation sampling and is a co-author of the manuscript presented in chapter 2 of this thesis. Dr. Vladimir Romanovsky helped with the analysis of temperature data and is a co-author of the chapter 3 manuscript.

Finally, I thank my family, friends and colleagues for all their emotional support. I am especially grateful for my husband Eamon O'Regan, who supported and encouraged me with endless patience, hugs and candy.

CHAPTER 1: GENERAL INTRODUCTION

INTRODUCTION

Nonsorted circles are unique patterned-ground features that dot the landscape of many arctic regions (Fig. 1.1). They are flat to dome-shaped, bare soil patches 0.5 to 3 m across and lack a border of stones (Fig. 1.2). These unusual features and their puzzling patterns have intrigued many researchers in the past, who have also used the synonymous terms frost scars (Sigafoos, 1951; Johnson and Neiland, 1983), frost boils (Gartner *et al.*, 1986; Chernov and Matveyeva, 1997; Walker *et al.*, 2004), mud boils (Zoltai and Tarnocai, 1981), spot medallions (Popov *et al.*, 1963) and Fleckentundra (Troll, 1944).

Nonsorted circles have complex origins, involving self-organization due to thermal instabilities in the soil that are combined with biological and physical feedbacks, shaping the morphology of these features. These morphologies are strongly influenced by the local climate and hydrological conditions. This study defines the nonsorted-circle system as the unit composed of the circle and inter-circle area along with the vegetation, soil and freezing and thawing water therein, and the upper part of the permafrost table (Fig. 1.3). Localized soil disturbances due to cryogenic processes (frost heave and needle-ice formation in the center of the nonsorted circles) create unusual micro-environments with unique plant communities, slow soil development and deep active layers. Thus, nonsorted circles offer an ideal natural system to study the complex linkages among vegetation, soil and cryogenic regime, and they provide insight into how the tundra system functions. The arctic tundra in northern Alaska varies along a natural existing climate gradient. As one moves from north to south, the mean July temperature increases from about 6 °C at the coast to about 12 °C at tree line, and the vegetation

changes from hemi-prostrate dwarf-shrub tundra to low shrub, tussock tundra (Walker, 2000). Understanding the response of naturally disturbed and undisturbed tundra along the arctic climate gradient will help in predictions of how climate change and anthropogenic disturbances will affect arctic systems.

STUDY OBJECTIVE

Several aspects of nonsorted circles have been studied in the past, such as the geomorphology (Washburn, 1956; Tedrow, 1977; Washburn, 1980; Zoltai and Tarnocai, 1981), self-organization (Hallet, 1990; Peterson and Krantz, 1998; Peterson and Krantz, 2003), soil instability and cryoturbation (Sigafoos, 1951; Gartner *et al.*, 1986; Ping *et al.*, 1998; Ping *et al.*, 2002; Haugland and Beatty, 2005), and vegetation patterns (Johnson and Neiland, 1983; Chernov and Matveyeva, 1997; Walker *et al.*, 2004). However, no study to date has treated nonsorted circles and their interactions with the surrounding stable tundra as a single complex system. Also, the role of nonsorted circles in ecosystem dynamics at multiple scales has not been studied. The contrast between barren nonsorted circles and the well-vegetated stable tundra provides a good opportunity to examine the linkages and feedbacks among vegetation, soil and cryogenic regime. The central goal of this thesis is to understand the interactions among vegetation, soils and cryogenic activity of nonsorted circles along a climate gradient in the Alaskan arctic tundra at different scales, ranging from the plot level to regional changes.

FORMATION OF NONSORTED CIRCLES

Although there has been considerable work describing the geomorphology of nonsorted circles (Washburn, 1956; Washburn, 1980; Zoltai and Tarnocai, 1981), their mode of formation is only partially understood. They are found in fine-grained soils associated with permafrost, and the formation is primarily driven by processes associated with the freezing and thawing of water (Washburn, 1980). Nonsorted circles are a product of differential frost heave due to environmental heterogeneity. Freezing in moist fine-grained soils is a non-homogeneous process, involving the process of water transport to the freezing front and the growth of distinct ice lenses (Hallet, 1990). The formation of ice lenses within the active layer leads to soil expansion in the winter, and the amount of soil heave is controlled by the advance of the freezing front (Hallet and Prestrud, 1986; Kessler *et al.*, 2001). Patterned-ground features such as nonsorted circles form when a physical instability in the frost-heave process occurs due to environmental heterogeneity and leads to differential frost heave (Peterson and Krantz, 2003). Peterson (1999) developed a model for differential frost heave that is based on soils undergoing top-down freezing, with the frozen fringe (or freezing front) separating the upper frozen soil with extensive ice lenses from the lower unfrozen, saturated soil. Perturbations of the ground and the freezing front cause some areas to heave differentially more than others. Once the pattern of differential frost heave is initiated, nonsorted circles may develop in certain soil conditions, and a patterned-ground landscape evolves. Nonsorted circles continue to heave differentially more than the surrounding tundra due to deeper thaw and more ice lenses in the barren circles and migration of water from the inter-circle areas. Peterson *et*

al. (2003) used the differential frost heave model to predict the magnitude of heave and the spacing and size of nonsorted circles, and they found that colder ground-surface temperatures result in greater frost heave. Thus, the vegetation cover has a constraining effect on frost heave and the development of nonsorted circles. Within the barren nonsorted circles, needle-ice formation at the ground surface may cause disturbance of the soil and vegetation. Needle ice forms at the surface of bare soils when steep temperature gradients exist, lifting the top soil layer off the ground (Troll, 1944; Mackay and Mathews, 1974; Washburn, 1980).

COMPLEXITY OF THE FROST-HEAVE SYSTEM

Once nonsorted circles are formed, they are self-perpetuating in nature and display tight linkages among vegetation, soil and cryogenic regime. Their character, however, changes over long periods of time due to changes in the thermal regime caused by the vegetation. This thesis treats the soil, vegetation and cryosphere of nonsorted circles as a single linked ecosystem. The hypothetical interactions among the system components are shown in Fig. 1.4. The vegetation and soil are linked through organic matter input to the soil and supply of mineralized nutrients to the plants. In stable tundra with thick vegetation mats and organic horizons, biological processes dominate, and physical disturbance by heave and needle-ice formation is minimal. In contrast, vegetation and soil organic layers are not dominant components of the barren nonsorted-circle system. The cryogenic regime of frost-heave features, as indicated by differential

heave, thaw depth and needle-ice formation, determines the type of vegetation and quantity of plant biomass that can be supported on the circles.

On the nonsorted circles, seasonal soil disturbances through frost heave and needle-ice formation mechanically damage roots, reduce seedling establishment and delay successional trends (Sigafoos, 1951; Johnson and Neiland, 1983; Jonasson and Sköld, 1983; Anderson and Bliss, 1998; Haugland and Beatty, 2005). Cryogenic processes also affect plants indirectly by altering the local microtopography, which in turn affects winter snow accumulation patterns, soil moisture and surface temperatures (Sigafoos, 1951; Johnson and Neiland, 1983). The bare to thinly vegetated nonsorted circles are poorly insulated, leading to greater temperature extremes at the soil surface, deeper summer thaw, and enhanced ice-lens formation and frost heaving, thus reinforcing the strong effect of cryogenic processes on vegetation.

In contrast to the barren nonsorted circles, the thick vegetation mats and organic horizons of the adjacent stable tundra insulate and shade the underlying mineral soil. For example, Beringer *et al.* (2001) modeled soil temperatures at 0.5 m depth of various tundra soils for northern Alaska. Their results show that a 25-cm thick moss and peat layer insulates the underlying soil, lowering soil temperatures by 6.9 °C in the summer when compared to a homogenous loam soil column. Pavlov and Moskalenko (2002) monitored the thermal regime of tundra soils on the Yamal Peninsula in Western Siberia and estimated that a 5 cm thick vegetation and litter layer cools soil temperatures by 0.5-1.5 °C, delaying soil thawing in the summer. The insulatve effect on the underlying mineral soil should decrease thaw depth and frost heaving in the stable tundra.

Physical soil properties such as soil moisture, porosity, aggregation and texture also affect cryogenic processes by influencing water movement and ice-lens formation in the soil. In turn, cryogenic processes can affect the soil through the uplift and subsequent weathering of mineral soils, increasing the soil pH. Cryogenic action may also break soil aggregates, disrupt the soil organic layer and move soil organic material downward through the profile due to churning motions. This thesis examines how these processes vary along a natural climate gradient in northern Alaska. The strength of the interactions discussed here should vary along the climate gradient, with cryogenic activity being a dominant process on nonsorted circles in the north, and biological interactions between vegetation and soil being important in the south. Also, the contrast between the nonsorted circles and the adjacent tundra should change along the climate gradient. In the northern sites, the contrast between the barren circles and the vegetated tundra should be great, whereas the contrast should decrease with increasing vegetation on the circles towards the south.

VEGETATION OF THE ARCTIC TUNDRA

Arctic tundra regions receive a low annual radiation input, resulting in cold air and soil temperatures, the presence of permafrost and a short snow-free season for plant growth (Chapin and Shaver, 1985; Bliss and Matveyeva, 1992). Therefore, tundra vegetation is dominated by hardy dwarf shrubs, perennial cushion forbs, grasses, sedges, mosses and lichens. Although the arctic flora in general is species-poor, the arctic tundra in northern Alaska is relatively rich in vascular species due to the Beringian land bridge

during the late Tertiary, which served as immigration route for Asian taxa and as an unglaciated refugium for regional species during the Pleistocene (Murray, 1992). The vegetation of the North Slope, Alaska, can be broadly divided into lowland tundra on the Coastal Plain and upland tundra in the Arctic Foothills. The lowland tundra is found on moist to wet nonacidic or acidic soils and is dominated by sedges and mosses, while the upland tundra consists of tussock sedges and thick moss carpets on acidic substrates. The vegetation also varies along soil moisture gradients, with low-diversity and high-productivity graminoid and moss stands dominating wet sites, and high-diversity, low-productivity vegetation consisting of dwarf shrubs, caespitose graminoids, cushion forbs and lichens growing on dry, exposed sites (Webber *et al.*, 1980).

Several studies have described the various vegetation types of northern Alaska (Hanson, 1953; Churchill, 1955; Bliss, 1956; Spetzman, 1959; Britton, 1965; Young, 1974; Racine, 1976; Webber, 1978; Walker, 1985; Walker and Everett, 1991; Walker *et al.*, 1991; Elias *et al.*, 1996). Most of these studies have used *ad hoc* criteria for the description and classification of plant communities. Only few studies in Alaskan arctic tundra regions have used the standard Braun-Blanquet approach accepted by the International Botanical Congress (Westhoff and van der Maarel, 1978). Walker *et al.* (1994) formally classified the tussock tundra on acidic slopes in the Arctic Foothills (Sphagno-Eriophoretum vaginati) and the zonal vegetation of the nonacidic moist tundra (Dryado integrifoliae-Caricetum bigelowii) in Alaska. Schickhoff *et al.* (2002) presented a formal classification of the riparian willow communities on the North Slope, Alaska. Komárková (1993) used the Braun-Blanquet approach to describe the vegetation of the

wet coastal plain at Atkasook, Alaska, but never published the final associations. Cooper (1986) classified the arctic-alpine tundra vegetation of the Arriegatch Creek Valley in the southern Brooks Range, Alaska. Outside of Alaska, there have been many arctic studies using the Braun-Blanquet approach. In the Canadian Arctic, Thannheiser (1976; 1991) described coastal and wetland plant communities, and Gould and Walker (1999) analyzed the vegetation of the Hood River corridor in the Northwest Territories. In the Russian Arctic, Matveyeva (1994) classified several tundra communities on the Taymir Peninsula. Noteworthy is also the study by Lünterbusch and Daniëls (2004) in Greenland.

A common framework of arctic vegetation built on the Braun-Blanquet classification approach enables better international circumpolar comparison and extrapolation of site measures of ecosystem dynamics to larger areas. In this thesis, I use the Braun-Blanquet approach to formally describe the plant communities associated with frost-disturbed and stable tundra on the Alaskan North Slope. I also place the plant associations into the global framework of vegetation orders and classes.

SUCCESSION, STRUCTURE AND DIVERSITY OF VEGETATION ON NONSORTED CIRCLES

With major soil movement occurring twice a year, the arctic tundra is characterized by a disturbance regime of high frequency and relatively strong severity. The unstable soil of nonsorted circles delays plant succession as it mechanically disturbs the development of plant roots and damages the vegetation cover (Chernov and Matveyeva, 1997; Anderson and Bliss, 1998), but it may also be important in providing

the main opportunity for seedling regeneration (Gartner *et al.*, 1986; Gough, 2006). On highly disturbed nonsorted circles, plant populations rarely progress beyond the initial invasion phase of succession (Svoboda and Henry, 1987), and plant succession does not occur in a directional or progressive sense but rather traces the year-to-year climatic changes (Johnson and Neiland, 1983). The repeated disturbance of the vegetation through cryogenic processes is inherent in the cycle, and a climax community may not be reached (Webber, 1978). On less active nonsorted circles, plant establishment usually occurs at the border positions, and over time, vegetation encroaches inward towards the disturbed centers (Haugland and Beatty, 2005). Succession within the patterned-ground features exhibits several stages (Chernov and Matveyeva, 1997; Haugland and Beatty, 2005; Michaelson *et al.*, 2005). The pioneers are bryophytes and nitrogen-fixing cryptogamic crusts, which ameliorate and stabilize the microsite environment. With increased nutrient and moisture supply, graminoid species establish themselves, followed by dwarf shrubs.

Root morphology may play an important role in governing the plant distributions along cryoturbation gradients. On King Christian Island in the Canadian High Arctic, Bell and Bliss (1978) reported that plants with multiple, fibrous roots and high rates of root turnover are more common in disturbed soils than plants with large roots and low root turnover rates. Similarly in northern Sweden, Jonasson and Sköld (1983) found that rhizomatous plants are mostly limited to stable soils in polygon fields, while herbaceous, fibrous-rooted plants are more frequent in disturbed nonsorted circles. Walker (1985) noted that the distribution of cushion forbs, caespitose graminoids and lichens is positively correlated with frost disturbance on the Alaskan North Slope.

The environmental heterogeneity associated with patterned ground may increase species diversity and richness due to variations in microtopography, soil moisture and nutrient regimes, creating a wide array of potential niches. Varying degrees of cryogenic action over a larger area generate a mosaic of plant species and communities of different successional stages, increasing species diversity and richness. Intermediate levels of disturbance through cryogenic activity could theoretically increase species diversity by providing competitor-free areas for plant colonization, whereas mild soil disturbance might allow for further successional stages to occur. Fox (1981) studied the effect of frost disturbance on the alpine vegetation of the White Mountains, Alaska, and found that several pioneer species colonized the mineral soil where it had been exposed due to disturbance. He reported that intermediate levels of frost disturbance maximized the plant diversity. The vegetation analysis portion of this thesis addresses how plant communities and species diversity of nonsorted circles and stable tundra vary along the climate gradient.

SOIL CHARACTERISTICS OF ARCTIC TUNDRA AND NONSORTED CIRCLES

Arctic tundra soils are characterized by the presence of permafrost, cold soil temperatures and cryoturbated profiles with warped or discontinuous soil horizons (Ping *et al.*, 1998). Despite low precipitation, soils in the rooting zone are generally wet, with the volumetric water content usually above 40% (Gersper *et al.*, 1980; Ping *et al.*, 1998), because the shallow depth to the permafrost table prevents drainage. The seasonal perching of the water table over permafrost and irregular soil moisture content associated

with the microtopography cause reduction-oxidation processes in the soil, and most permafrost soils display gleyed mineral horizons with reduced colors (Tedrow, 1977; Höfle *et al.*, 1998; Ping *et al.*, 1998). Decomposition of organic matter in arctic soils is very slow due to the saturated soils, low soil temperatures and recalcitrant organic plant material, resulting in the gradual accumulation of organic matter (Gersper *et al.*, 1980; Chapin and Shaver, 1985; Ping *et al.*, 1998). Chapin *et al.* (1988) estimated extremely slow rates of mineralization and nutrient turnover of up to 40 to 90 years in arctic tussock tundra in Northern Alaska. Thus, arctic tundra soils store great amounts of carbon, most of it locked up in the permafrost due to frost-churning processes that move the organic material downward through the profile and the aggrading permafrost table that moves upward (Ping *et al.*, 1997). For example, Ping *et al.* (1997) calculated the average organic carbon storage of the arctic tussock tundra pedon in northern Alaska to be about 600 MgC/ha.

Nutrient availability is low in arctic soils because low precipitation limits atmospheric input, and low temperatures prevent chemical weathering of parent material. In addition, low temperatures and poor aeration minimize nitrogen fixation and the rate of nutrient release from organic matter (Chapin and Shaver, 1985). Nutrients have a long residence time in the soil and are immobilized by soil microorganisms (Jonasson *et al.*, 1999). Nitrogen is the most limiting nutrient in arctic tundra systems. Although the arctic tundra is often assumed to be an ammonia-dominated ecosystem (Gersper *et al.*, 1980; Everett *et al.*, 1981), Atkin (1996) demonstrated that several sources of soil nitrogen are available to arctic plants, including soluble organic nitrogen, ammonia and nitrate.

Ammonia is the superior source of nitrogen for plants and the uptake is not very cold sensitive, but most tundra plants, especially in symbiosis with ectomycorrhizae, also take up soluble organic nitrogen and inorganic nitrate. Arctic plants often reduce their dependence on soil nitrogen uptake through internal recycling of nitrogen. They withdraw nitrogen from senescing leaves and redistribute it to newly developing plant parts (Atkin, 1996).

The biogeochemistry of arctic soils is closely related to the vegetation types of the arctic ecosystem. Arctic tundra varies widely in dominant plant growth forms, with growth forms differing significantly in their patterns of tissue turnover rates and internal element cycling (Stoner *et al.*, 1982). Verville *et al.* (1998) conducted a plant species removal experiment to assess the influence of vegetation types on methane and carbon dioxide flux in Alaskan arctic tundra. Moss removal in wet meadows increased methane emissions while removal of sedges decreased methane flux, suggesting that sedges contribute to methane emissions by transporting methane from anaerobic soil to the atmosphere. Different plant functional types did not affect carbon dioxide flux. Judd and Kling (2002) found that vegetation type also influences dissolved carbon export from tundra ecosystems. Dissolved carbon production and export rates in Alaskan tundra were greatest for inter-tussock areas, moderate in tussock areas and lowest in wet sedge environments. However, Dormann and Woodin (2002) performed a meta-analysis of field experiments using plant functional types and found that arctic plant species differed so widely in their response to environmental factors that no generalizations of plant functional types and their effect on biogeochemistry could be made.

Nonsorted circles differ from the surrounding stable tundra in several soil characteristics, having thinner organic horizons, greater bulk densities and lower soil moisture than the adjacent tundra (Zoltai and Tarnocai, 1981; Walker *et al.*, 2004). The mineral soils of the nonsorted circles have greater pH values due to soil mixing with upheaved mineral soil and enhanced weathering (Jonasson and Sköld, 1983; Tarnocai, 2004; Michaelson *et al.*, 2005). Cryogenic processes influence the biogeochemical cycle within nonsorted circles. Parts of the organic soil from the adjacent stable tundra are churned into the soil of the nonsorted circles through soil movement and leaching, affecting the decomposition and mineralization within nonsorted circles (Fig. 1.5). Jonasson and Sköld (1983) reported greater soil nutrient concentrations in active nonsorted circles when compared to the adjacent stable tundra, which may be an important factor determining plant distributions in patterned-ground systems. On the other hand, Walker *et al.* (2004) found less plant-available nutrients and lower C/N ratios in nonsorted circles when compared to the adjacent tundra. Nonsorted circles and the associated nitrogen-fixing species may play a key role in the nitrogen dynamics of tundra ecosystems, which are generally nitrogen-limited (Chapin *et al.*, 1995).

Although this thesis focuses on vegetation, it also provides considerable insight to how the vegetation modifies the soil through time on stable surfaces and how climate affects these processes.

INFLUENCE OF CLIMATE ON THE MORPHOLOGY OF NONSORTED CIRCLES

The influence of vegetation succession and cryogenic processes on the morphology of patterned-ground features varies strongly along the arctic climate gradient (Chernov and Matveyeva, 1997; Walker *et al.*, 2004). Chernov and Matveyeva (1997) have perceptively portrayed the transitions in vegetation and small patterned-ground morphologies along the arctic climate gradient (Fig. 1.6). In the High Arctic, contraction cracking due to desiccation and/or freezing processes is a dominant process (Washburn, 1980), and it forms small polygons 10-20 cm across. The physical constraints of the harsh environment result in bare frost-heave features. Small mosses and herbaceous plants are often restricted to protected sites in the cracks between polygons. Differential frost heave affects the patterned ground most strongly in the Mid Arctic. Here, physical processes dominate on frost-heave features and result in sparse vegetation on the edges of the nonsorted circles, and biological processes dominate in the adjacent tundra due to the moderate climate, allowing for denser vegetation and thicker organic layers. Farther south in the Low Arctic, biological processes dominate the landscape morphology and result in well vegetated nonsorted circles that often are hard to differentiate from the surrounding tundra.

The interactions among the components of the frost-heave system are driven by the regional climate. Nonsorted circles seem to emerge only under certain environmental conditions and are therefore highly susceptible to environmental change (Walker *et al.*, 2004). Climate is predicted to warm most dramatically at high latitudes in response to global atmospheric change (Houghton *et al.*, 1996; Intergovernmental Panel on Climate

Change (IPCC), 2001; Johannessen *et al.*, 2004), and climate change in arctic ecosystems is expected to have major effects on vegetation patterns, permafrost regimes and nutrient cycling (Chapin *et al.*, 2004; Hinzman *et al.*, 2005; Sturm *et al.*, 2005). An alteration of temperature and moisture regimes caused by global climate change will likely result in shifts of vegetation zones and species composition (Chapin *et al.*, 1995; Epstein *et al.*, 2000). A potential decline in cryoturbation activity due to increased biomass could lead to local disappearance of frost-heave features in the arctic tundra and a decrease in landscape heterogeneity and biodiversity.

ORGANIZATION OF THESIS

In the first chapter of this thesis, I examine the role of vegetation in shaping nonsorted circles and the variations along the climate gradient (Table 1.1). I study the plant community structure and composition of nonsorted circles and the relationships between vegetation and the environment as a critical foundation to understand the patterned-ground system and its potential responses to global climate change. The major research questions are: (a) What are the plant communities on and off the nonsorted circles in the Alaskan arctic tundra? (b) What are the environmental gradients determining the composition and structure of the communities? (c) How do the plant communities and the morphology of the nonsorted circles change along the climate gradient? I present a formal description and analysis of the plant communities on and in between frost-heave features along a climatic gradient using the Braun-Blanquet approach (Westhoff and van der Maarel, 1978; Dierschke, 1994). I place the plant

communities into the larger framework of vegetation orders and classes, which lays the foundation for further arctic vegetation classification and vegetation modeling work. I relate soil and environmental variables to the plant communities through Detrended Correspondence Analysis (Hill and Gauch, 1980). I also investigate the changing strength of the interactions among vegetation, soil and cryogenic regime along the bioclimate gradient.

The second chapter focuses on how the vegetation affects the thermal regime of the soil. The influence of the plant canopy and soil organic horizons on soil temperatures is important to cryogenic processes. The vegetation and organic horizons insulate the soil and lower the summer temperatures at rooting depth. Although air temperatures increase towards the south along the climate gradient, soil temperature may not follow the same trend due to insulation. I use the temperature gradient as a common underlying variable in both the first and the second chapter: While the first chapter examines the biological aspects of the cryoturbated tundra system along the climate gradient, the second chapter focuses on the changes in the physical system properties. Here, I investigate how the vegetation and soil organic mat affect the microclimate of the nonsorted circles and the stable tundra, and how the interactions change along the climate gradient (Table 1.1). I quantify the effective insulation of vegetation and organic soil horizons on the mineral soil. I analyze how soil-surface temperatures, thaw depth, snow properties and soil moisture vary between nonsorted circles and the stable tundra and with respect to climate. I expect the thickness of the vegetation and soil organic layer to be negatively related to soil temperatures and thaw depth. Thus, the thaw depth might not be correlated with

summer air temperature as many models have suggested: It could be limited by cold temperatures in the north and thick insulative vegetation mats in the south, while the deepest thaw might occur under intermediate climate conditions.

In the third chapter, I examine how the vegetation affects the cryogenic regime of nonsorted circles with the help of an experiment and discuss the implications in the light of climate change (Table 1.1). I manipulate the plant canopy of nonsorted circles by (a) removing vegetation, (b) adding sedge transplants, or (c) adding a moss carpet. I study the influence of the vegetation on the soil thermal properties, thaw depth, frost heave and soil-surface stability of nonsorted circles. I hypothesize that vegetation removal will increase summer temperatures, thaw depth and potentially frost heave, while the addition of mosses to the nonsorted circles will decrease these variables. Cryostatic suction may pull water from the adjacent tundra into the nonsorted circles, increasing the amount of ice lenses and heave in the circles. I also investigate soil-surface instability, most likely due to needle-ice formation, using a "toothpick index" (Gartner *et al.*, 1986).

In the final synthesis chapter, I summarize the major findings of my thesis (Table 1.1). I also focus on the role of nonsorted circles on ecosystem dynamics and discuss the implication of nonsorted circles to a host of arctic system properties and functions, including plant and landscape diversity, nutrient cycling and carbon storage, trace-gas and energy fluxes to the atmosphere, water movement, animal use through forage quality, and human disturbance. I examine the potential effects of a warming arctic climate on several system properties of the nonsorted circles, such as biomass, nutrient availability, heat flux and frost heave, and I give suggestions for further research.

REFERENCES

Anderson DG, and Bliss LC. 1998. Association of plant distribution patterns and microenvironments on patterned ground in a polar desert, Devon Island, N.W.T., Canada. *Arctic and Alpine Research* **30**: 97-107.

Atkin OK. 1996. Reassessing the nitrogen relations of arctic plants: a mini-review. *Plant, Cell and Environment* **19**: 695-704.

Bell KL, and Bliss LC. 1978. Root growth in a polar semidesert environment. *Canadian Journal of Botany* **56**: 2470-2490.

Beringer J, Lynch AH, Chapin FS, III, Mack M, and Bonan GB. 2001. The representation of arctic soils in the land surface model: the importance of mosses. *Journal of Climate* **14**: 3324-3335.

Bliss LC. 1956. A comparison of plant development in microenvironments of arctic and alpine tundras. *Ecological Monographs* **26**: 303-337.

Bliss LC, and Matveyeva NV. 1992. Circumpolar arctic vegetation. In *Arctic ecosystems in a changing climate: an ecophysiological perspective*, Chapin FS, III, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J, and Chu EW (eds). Academic Press: San Diego; 59-89.

Britton ME. 1965. Vegetation of the Arctic tundra. In *Arctic biology*, Hanson HP (ed). Oregon State University Press: Corvallis, OR; 67-130.

Chapin FS, III, and Shaver GR. 1985. Arctic. In *Physiological ecology of North American plant communities*, Chabot BF, and Mooney HA (eds). Chapman and Hall: New York; 16-40.

Chapin FS, III, Fetcher N, Kielland K, Everett KR, and Linkins AE. 1988. Productivity and nutrient cycling of Alaskan tundra: enhancement by flowing soil water. *Ecology* **69**: 693-702.

Chapin FS, III, Peterson G, Berkes F, Callaghan TV, Angelstam P, Apps M, Beier C, Bergeron Y, Crépin A-S, Danell K, Elmqvist T, Folke C, Forbes B, Fresco N, Juday G, Niemelä J, Shvidenko A, and Whiteman G. 2004. Resilience and vulnerability of northern regions to social and environmental change. *Ambio* **33**: 344-349.

Chapin FS, III, Shaver GR, Giblin AE, Nadelhoffer KG, and Laundre JA. 1995. Response of arctic tundra to experimental and observed changes in climate. *Ecology* **76**: 694-711.

Chernov YI, and Matveyeva NV. 1997. Arctic ecosystems in Russia. In *Ecosystems of the world, vol. 3: Polar and alpine tundra*, Wielgolaski FE (ed). Elsevier: Amsterdam; 361-507.

Churchill ED. 1955. Phytosociological and environmental characteristics of some plant communities in the Umiat region of Alaska. *Ecology* **36**: 606-627.

Cooper DJ. 1986. Arctic-alpine tundra vegetation of the Arrigetch Creek Valley, Brooks Range, Alaska. *Phytocoenologia* **14**: 467-555.

Dierschke H. 1994. *Pflanzensoziologie*. Ulmer Verlag: Stuttgart.

Dormann CF, and Woodin SJ. 2002. Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. *Functional Ecology* **16**: 4-18.

Elias SA, Short SK, Walker DA, and Auerbach NA. 1996. Final report: historical biodiversity at remote Air Force sites in Alaska. Legacy Resource Management Program Project, 0742, Department of Defense, Air Force.

Epstein HE, Walker MD, Chapin FS, III, and Starfield AM. 2000. A transient, nutrient-based model of arctic plant community response to climate warming. *Ecological Applications* **10**: 824-841.

Everett KR, Vassiljevskaya VD, Brown J, and Walker BD. 1981. Tundra and analogous soils. In *Tundra ecosystems: a comparative analysis*, Bliss LC, Heal OW, and Moore JJ (eds). Cambridge University Press: Cambridge; 139-179.

Fox JF. 1981. Intermediate levels of soil disturbance maximize alpine plant diversity. *Nature* **293**: 564-565.

Gartner BL, Chapin FS, III, and Shaver GR. 1986. Reproduction of *Eriophorum vaginatum* by seed in Alaskan tussock tundra. *Journal of Ecology* **74**: 1-18.

Gersper PL, Alexander V, Barkley SA, Barsdate RJ, and Flint PS. 1980. The soils and their nutrients. In *An arctic ecosystem: the coastal tundra at Barrow, Alaska*, Brown J, Miller PC, Tieszen LL, and Bunnel FL (eds). Dowden, Hutchinson and Ross, Inc.: Stroudburg, PA; 219-254.

Gough L. 2006. Neighbor effects on germination, survival, and growth in two arctic tundra plant communities. *Ecography* **29**: 1-13.

Gould WA, and Walker MD. 1999. Plant communities and landscape diversity along a Canadian Arctic river. *Journal of Vegetation Science* **10**: 537-548.

Hallet B. 1990. Self-organization in freezing soils: from microscopic ice lenses to patterned ground. *Canadian Journal of Physics* **68**: 842-852.

Hallet B, and Prestrud S. 1986. Dynamics of periglacial sorted circles in western Spitzbergen. *Quaternary Research* **26**: 81-99.

Hanson HC. 1953. Vegetation types in northwestern Alaska and comparisons with communities in other arctic regions. *Ecology* **34**: 111-148.

Haugland JE, and Beatty SW. 2005. Vegetation establishment, succession and microsite frost disturbance on glacier forelands within patterned ground chronosequences. *Journal of Biogeography* **32**: 145-153.

Hill MO, and Gauch HG. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* **42**: 47-58.

Hinzman LD, Bettez ND, Bolton WR, Chapin FS, III, Dyurgerov MB, Fastie CL, Griffith B, Hollister RD, Hope A, Huntington HP, Jensen AM, Jia GJ, Jorgenson T, Kane DL, Klein DR, Kofinas G, Lynch AH, Lloyd AH, McGuire AD, Nelson FE, Oechel WC, Osterkamp TE, Racine CH, Romanovsky VE, Stone RS, Stow DA, Sturm M, Tweedie CE, Vourlitis GL, Walker MD, Walker DA, Webber PJ, Welker JM, Winker KS, and Yoshikawa K. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change* **72**: 251-298.

Höfle C, Ping CL, and Kimble JM. 1998. Properties of permafrost soils on the northern Seward Peninsula, Northwest Alaska. *Soil Science Society of America Journal* **62**: 1629-1639.

Houghton JT, Meira Filho LG, Callandar BA, Harris N, Kattenberg A, and Maskell K. 1996. *Climate change 1995: the science of climate change*. Cambridge University Press: Cambridge.

Intergovernmental Panel on Climate Change (IPCC). 2001. *Climate change 2000, third assessment report*. Cambridge University Press: Cambridge.

Johannessen OM, Bengtsson L, Miles MW, Kuzmina SI, Semenov VA, Alekseev GV, Nagurnyi AP, Zakharov VF, Bobylev LP, Pettersson LH, K. H, and Cattle HP. 2004. Arctic climate change: observed and modeled temperature and sea-ice variability. *Tellus* **56A**: 328-341.

Johnson AW, and Neiland BJ. 1983. An analysis of plant succession on frost scars 1961-1980. Proceedings on Permafrost: Fourth International Conference. National Academy Press: University of Alaska Fairbanks, Fairbanks.

Jonasson S, Michelsen A, and Schmidt IK. 1999. Coupling of nutrient cycling and carbon dynamics in the Arctic: integration of soil microbial and plant processes. *Applied Soil Ecology* **11**: 135-146.

Jonasson S, and Sköld SE. 1983. Influences of frost-heaving on vegetation and nutrient regime of polygon-patterned ground. *Vegetatio* **53**: 97-112.

Judd KE, and Kling GW. 2002. Production and export of dissolved C in arctic tundra mesocosms: the roles of vegetation and water flow. *Biogeochemistry* **60**: 213-234.

Kessler MA, Murray AB, and Werner BT. 2001. A model for sorted circles as self-organized patterns. *Journal of Geophysical Research* **106**: 13287-13306.

Komárková V. 1993. Vegetation type hierarchies and landform disturbance in arctic Alaska and alpine Colorado with emphasis on snowpatches. *Vegetatio* **106**: 155-181.

Lünterbusch CH, and Daniëls FJA. 2004. Phytosociological aspects of *Dryas integrifolia* vegetation on moist-wet soil in Northwest Greenland. *Phytocoenologia* **34**: 241-270.

Mackay JR, and Mathews WH. 1974. Needle ice striped ground. *Arctic and Alpine Research* **6**: 79-84.

Matveyeva NV. 1994. Floristic classification and ecology of tundra vegetation of the Taymyr Peninsula, northern Siberia. *Journal of Vegetation Science* **5**: 813-838.

Michaelson GJ, Ping CL, and Walker DA. 2005. Biogeochemistry of soils associated with cryptogamic crusts on frost boils in arctic Alaska. *Arctic, Antarctic and Alpine Research*: (in review).

Murray DF. 1992. Vascular plant diversity in Alaskan arctic tundra. *Northwest Environmental Journal* **8**: 29-52.

Pavlov AV, and Moskalenko NG. 2002. The thermal regime of soils in the north of Western Siberia. *Permafrost and Periglacial Processes* **13**: 43-51.

Peterson RA. 1999. Differential frost heave manifest as patterned ground-modeling, laboratory and field studies. Ph.D. Thesis, University of Colorado, Boulder.

Peterson RA, and Krantz WB. 1998. A linear stability analysis for the inception of differential frost heave. In *Proceedings of the Seventh International Conference on Permafrost*, Yellowknife, Canada; 883-889.

Peterson RA, and Krantz WB. 2003. A mechanism for differential frost heave and its implications for patterned ground formation. *Journal of Geology* **49**: 69-80.

Peterson RA, Walker DA, Romanovsky VE, Knudson JA, Raynolds MK, and Krantz WB. 2003. A differential frost heave model: cryoturbation-vegetation interactions. In *Proceedings of the Eighth International Conference on Permafrost*, Zürich, Switzerland; 885-890.

Ping CL, Bockheim JG, Kimble JM, Michaelson GJ, and Walker DA. 1998. Characteristics of cryogenic soils along a latitudinal transect in Arctic Alaska. *Journal of Geophysical Research* **103**: 28917-28928.

Ping CL, Michaelson GJ, and Kimble JM. 1997. Carbon storage along a latitudinal transect in Alaska. *Nutrient Cycling in Agroecosystems* **49**: 235-242.

Ping CL, Michaelson GJ, Kimble JM, Shur YL, and Walker DA. 2002. Morphogenesis of soils associated with frost boils. *Eos Transactions AGU* **83**: Supplement F259.

Popov MV, Kachurin SP, and Grave NA. 1963. Features of the development of frozen geomorphology in northern Eurasia. In *Proceedings of Permafrost International Conference*, Lafayette; 43-50.

Racine C. 1976. Flora and vegetation. In *Biological survey of the proposed Kobuk Valley National Monument*, Melchior H (ed). National Park Service, U.S. Department of the Interior: University of Alaska, Fairbanks; 39-135.

Schickhoff U, Walker MD, and Walker DA. 2002. Riparian willow communities on the Arctic Slope of Alaska and their environmental relationships: A classification and ordination analysis. *Phytocoenologia* **32**: 145-204.

Sigafoos RS. 1951. Soil instability in tundra vegetation. *Ohio Journal of Science* **6**: 281-298.

Spetzman LA. 1959. Vegetation of the arctic slope of Alaska. U.S. Geological Survey Professional Paper 302-B. U.S. Government Printing Office: Washington, DC.

Stoner WA, Miller P, and Miller PC. 1982. Seasonal dynamics and standing crops of biomass and nutrients in a subarctic tundra vegetation. *Holarctic Ecology* **5**: 172-179.

Sturm M, Schimel J, Michaelson G, Welker JM, Oberbauer SF, Liston GE, Fahnestock J, and Romanovsky VE. 2005. Winter biological processes could help convert arctic tundra to shrubland. *BioScience* **1**: 17-26.

Svoboda J, and Henry GHR. 1987. Succession in marginal arctic environments. *Arctic and Alpine Research* **19**: 373-384.

Tarnocai C. 2004. Classification of Cryosols in Canada. In *Cryosols: permafrost-affected soils*, Kimble JM (ed). Springer-Verlag: New York; 599-610.

Tedrow JCF. 1977. *Soils of the polar landscapes*. Rutgers University Press: New Brunswick, NJ.

Thannheiser D. 1976. Ufer- und Sumpfvegetation auf dem westlichen kanadischen Arktis-Archipel und Spitzbergen. *Polarforschung* **46**: 71-82.

Thannheiser D. 1991. Die Küstenvegetation der arktischen und borealen Zone. *Berichte der Reinhold-Tüxen-Gesellschaft* **3**: 21-42.

Troll C. 1944. Strukturböden, Solifluktion und Frostklimate der Erde. *Geologische Rundschau* **34**: 545-694.

Verville JH, Hobbie SE, Chapin FS, III, and Hooper DU. 1998. Response of tundra CH_4 and CO_2 flux to manipulation of temperature and vegetation. *Biogeochemistry* **41**: 215-235.

Walker DA. 1985. Vegetation and environmental gradients of the Prudhoe Bay region, Alaska. CRREL Report 85-14

Walker DA. 2000. Hierarchical subdivision of arctic tundra based on vegetation response to climate, parent material and topography. *Global Change Biology* **6**: 19-34.

Walker DA, Epstein HE, Gould WA, Kelley AM, Kade A, Knudson JA, Krantz WB, Michaelson GJ, Peterson RA, Ping CL, Raynolds MK, Romanovsky VE, and Shur Y. 2004. Frost-boil ecosystems: complex interactions between landforms, soils, vegetation and climate. *Permafrost and Periglacial Processes* **15**: 171-188.

Walker DA, and Everett KR. 1991. Loess ecosystems of northern Alaska: regional gradient and toposequence at Prudhoe Bay. *Ecological Monographs* **61**: 437-464.

Walker MD, Walker DA, and Auerbach NA. 1994. Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska. *Journal of Vegetation Science* **5**: 843-866.

Walker MD, Walker DA, Everett KR, and Short SK. 1991. Steppe vegetation on south-facing slopes of pingos, central Arctic Coastal Plain, Alaska, U.S.A. *Arctic and Alpine Research* **23**: 170-188.

Washburn AL. 1956. Classification of patterned ground and review of suggested origins. *Bulletin of the Geological Society of America* **67**: 823-866.

Washburn AL. 1980. *Geocryology: A survey of periglacial processes and environments.* John Wiley and Sons: New York.

Webber PJ. 1978. Spatial and temporal variation of the vegetation and its production, Barrow, Alaska. In *Vegetation and production ecology of an Alaskan Arctic Tundra,* Tieszen LL (ed). Springer Verlag: New York; 37-112.

Webber PJ, Miller PC, Chapin FS, III, and McCown BH. 1980. The vegetation: pattern and succession. In *An arctic ecosystem: the coastal tundra at Barrow, Alaska,* Brown J, Miller PC, Tieszen LL, and Bunnel FL (eds). Dowden, Hutchinson and Ross, Inc.: Stroudsburg, PA; 186-218.

Westhoff V, and van der Maarel E. 1978. The Braun-Blanquet approach. In *Classification of plant communities,* Whittaker RH (ed). Junk: Den Haag; 287-399.

Young SB. 1974. Vegetation of the Noatak River valley. In *The environment of the Noatak River basin, Alaska,* Young SB (ed). Center for Northern Studies: Wolcott, VT; 58-84.

Zoltai SC, and Tarnocai C. 1981. Some nonsorted patterned ground types in northern Canada. *Arctic and Alpine Research* **13**: 139-151.

Table 1.1. Overview of the thesis components, questions and approach.

Chapter	Component	Questions	Approach
1	Biological aspects of patterned-ground system along climate gradient	a. What are the plant communities on and off nonsorted circles? b. How is the environment related to the vegetation? c. How do plant communities change along climate gradient?	a. Braun-Blanquet classification of plant communities. b. Ordination with Detrended Correspondence Analysis. c. Mapping of nonsorted circles at micro-scale.
2	Physical aspects of patterned-ground system along climate gradient	a. How do vegetation and organic mat affect microclimate of non-sorted circles and stable tundra? b. How do interactions between vegetation, soil, heave and thaw change along climate gradient?	a. Quantify effective insulation at soil surface using n-factor. b. Compare soil temperature and moisture, thaw, snow properties along climate gradient.
3	Link between vegetation and cryogenic regime	How does vegetation affect cryogenic activity of nonsorted circles?	Experimental alteration of plant canopy and monitoring soil temperature, thaw, heave.
4	Synthesis	What are the effects of nonsorted circles on the ecosystem and the implications of climate change?	Summary and application of results.

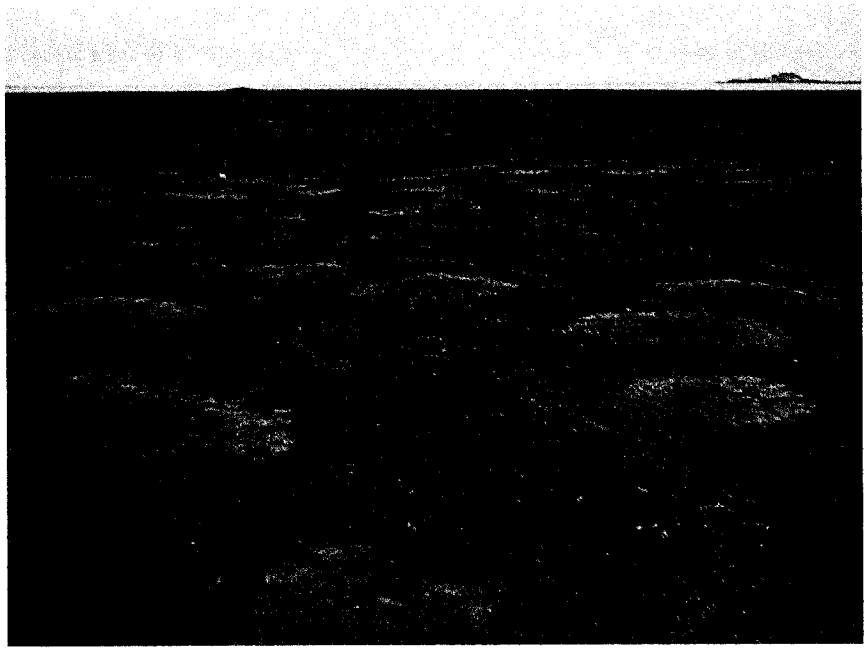

Fig. 1.1. Nonsorted circles on Howe Island, Alaska. The diameter of the nonsorted circles is 2-3 m.

Fig. 1.2. Typical nonsorted circle with barren patches on the Coastal Plain at Franklin Bluffs, Alaska.

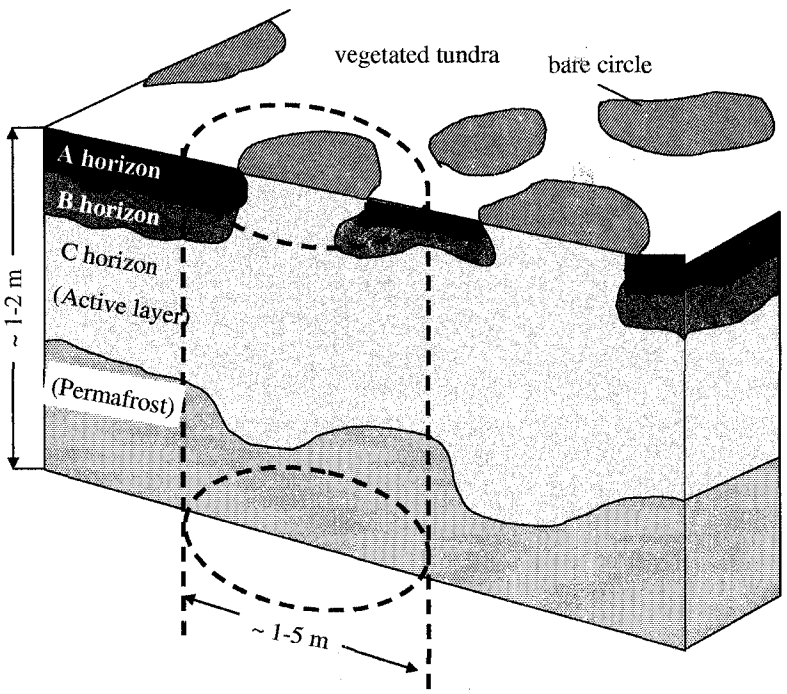

Fig. 1.3. Cross-section through a cryoturbated tundra profile showing a unit of the nonsorted-circle system. The vegetated areas have well-developed A and B horizons and a shallower active layer than the bare nonsorted circles. The cylinder shows the approximate scale of one complete unit of the nonsorted-circle system. Diagram adapted from Tarnocai (2004).

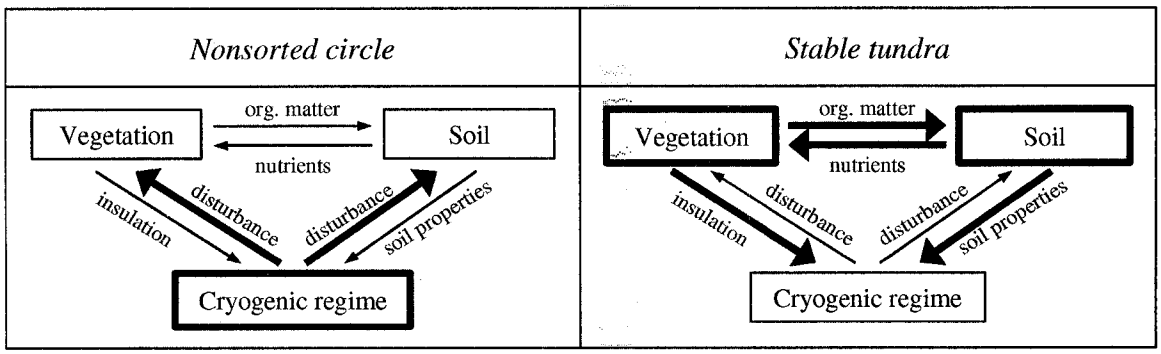

Fig. 1.4. Hypothesized interactions among major components of the frost-heave system (vegetation, soil and cryogenic regime) for the nonsorted circles and the adjacent stable tundra. The vegetation and soil are linked through the input of organic matter and the supply of nutrients. The vegetation affects the cryogenic regime negatively through shading and insulation, and in turn is disturbed through cryogenic activity. Also, soil organic layer, moisture and texture influence the cryogenic regime, which in turn affects the soil through disturbance. The degree of dominance of the component on the system is indicated by the boldness of the box, and the strength of interaction between the components is indicated by the boldness of the arrow. In the nonsorted circle, physical processes related to cryogenic processes (ice-lens and needle-ice formation) dominate. In the stable tundra, biological processes related to organic matter accumulation alter the thermal regime and act to stabilize the cryogenic processes. Diagram adapted from Walker *et al.* 2004.

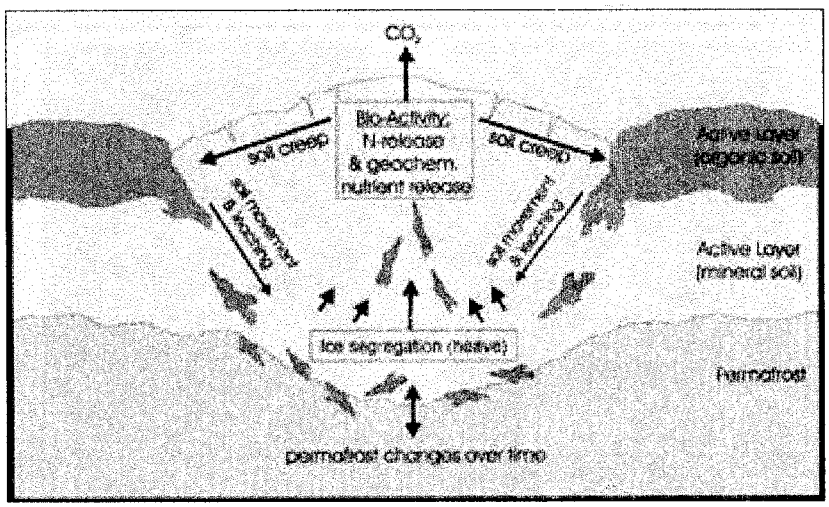

Fig. 1.5. Generalized biogeochemical cycle within a nonsorted circle. Frost heave affects decomposition and mineralization of organic matter from the adjacent tundra. Diagram after Walker *et al.* (2004).

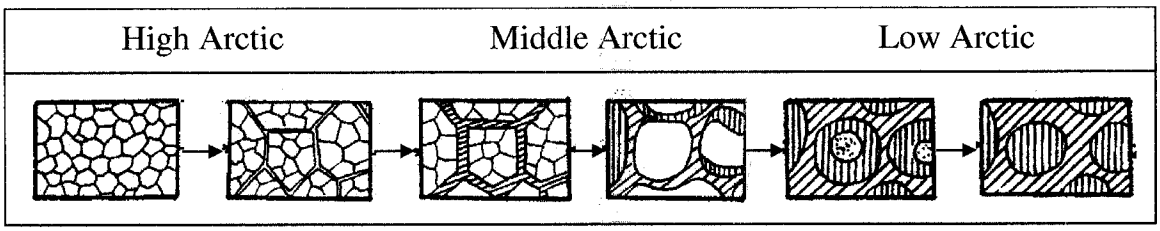

Fig. 1.6. Successional stages and the formation of nonsorted polygons (in the High to Middle Arctic) and nonsorted circles (in the Middle to Low Arctic) along the arctic climate gradient. In the High Arctic, bare soil with contraction cracks, which are sometimes populated by mosses and herbs, dominates the landscape. In the Middle Arctic, the cracks are filled with vegetation and pioneer species appear on the edges of the circles. In the Low Arctic, the centers of the nonsorted circles are almost fully vegetated. The High Arctic is equivalent to the bioclimate subzones A and B, the Middle Arctic to subzone C, and the Low Arctic to subzones D and E. Diagram adapted from Chernov and Matveyeva (1997).

CHAPTER 2: PLANT COMMUNITIES AND SOILS IN CRYOTURBATED TUNDRA ALONG A BIOCLIMATE GRADIENT IN THE LOW ARCTIC, ALASKA

* Published as: Kade A, Walker DA, and Raynolds MK. 2005. Plant communities and soils in cryoturbated tundra along a bioclimate gradient in the Low Arctic, Alaska. *Phytocoenologia* **35**: 761-820.

ABSTRACT

Nonsorted circles and earth hummocks are important landscape components of the arctic tundra. Here we describe the vegetation on these frost-heave features at seven study sites along a N-S-transect from the Arctic Ocean to the Arctic Foothills, Alaska. We established 117 relevés in frost-heave features and surrounding tundra and classified the vegetation according to the Braun-Blanquet sorted-table method. We used Detrended Correspondence Analysis to analyze relationships between vegetation and environmental variables. We identified nine communities: *Braya purpurascens-Puccinellia angustata* community (dry nonsorted circles, subzone C); *Dryas integrifolia-Salix arctica* community (dry tundra, subzone C); Salici rotundifoliae-Caricetum aquatilis ass. nov. (moist coastal tundra, subzone C); Junco biglumis-Dryadetum integrifoliae ass. nov. (moist nonsorted circles, subzone D); Dryado integrifoliae-Caricetum bigelowii Walker et al. 1994 (moist tundra, subzone D); *Scorpidium scorpioides-Carex aquatilis* community (wet tundra, subzone D); Cladino-Vaccinietum vitis-idaeae ass. nov. (dry nonsorted circles and earth hummocks, subzone E); Sphagno-Eriophoretum vaginati Walker et al. 1994 (moist tundra, subzone E); and *Anthelia juratzkana-Juncus biglumis* community (wet nonsorted circles, subzone E).

The DCA ordination displayed the vegetation types with respect to complex environmental gradients. The first axis of the ordination corresponds to a bioclimate/pH gradient, and the second axis corresponds to a disturbance/soil moisture gradient. Frost-heave features are dominated by lichens, whereas the adjacent tundra supports more dwarf shrubs, graminoids and mosses. Frost-heave features have greater thaw depths,

more bare ground, thinner organic horizons and lower soil moisture than the surrounding tundra. The morphology of frost-heave features changes along the climatic gradient, with large, barren nonsorted circles dominating the northern sites and vegetated, less active earth hummocks dotting the southern sites. Thawing of permafrost and a possible shift in plant community composition due to global warming could lead to a decline in frost-heave features and result in the loss of landscape heterogeneity.

INTRODUCTION

The vegetation and soil patterns in many arctic tundra regions are influenced by the distribution of frost-heave features such as nonsorted circles and earth hummocks (Washburn, 1980). Nonsorted circles and earth hummocks form in fine-grained soils with permafrost. Nonsorted circles are a form of patterned ground common in most arctic regions. They are more or less flat, bare soil patches 0.5 to 3 m across and lack a border of stones. These features are a product of differential frost heave, which occurs when ice lenses form in the soils during winter. Nonsorted circles heave more than the surrounding tundra due to deeper thaw and more ice lenses in the barren circles and also due to migration of water from the inter-circle areas (Peterson and Krantz, 2003). Earth hummocks are well-vegetated, mound-shaped landforms up to 50 cm tall and 1-2 m in diameter. They usually have a mineral soil core and are also often caused by differential frost heave. Another prevalent process in the Arctic is contraction cracking due to desiccation and/or freezing processes (Washburn, 1980). These contraction cracks form polygons, with diameter sizes ranging from centimeters to several meters. Small

nonsorted contraction-crack polygons up to 40 cm in diameter form in conjunction with nonsorted circles in the High Arctic and the northern portion of our gradient.

Several aspects of frost-heave features have been studied in the past, such as geomorphology (Washburn, 1956; Washburn, 1980), self-organization of patterned ground (Hallet and Prestrud, 1986; Hallet, 1990; Kessler *et al.*, 2001; Kessler and Werner, 2003; Peterson and Krantz, 2003; Peterson *et al.*, 2003), soil instability and cryoturbation (Sigafoos, 1951; Gartner *et al.*, 1986; Ping *et al.*, 1998; Walker *et al.*, 2004), and vegetation patterns (Johnson and Neiland, 1983; Chernov and Matveyeva, 1997; Walker *et al.*, 2004). However, no study to date has presented a formal description and analysis of the plant communities on these unique landforms. In this study, we classify and describe the plant communities on and in between frost-heave features along a climatic gradient in the Low Arctic in Alaska. We relate soil and environmental variables to the plant communities through Detrended Correspondence Analysis and discuss the implication of these relationships with respect to a changing arctic climate.

STUDY AREA

Location and climate

This study was conducted along a N-S-transect from the coast of the Arctic Ocean to the Arctic Foothills along the northern segment of the Dalton Highway, Alaska, close to the Sagavanirktok River (Fig. 2.1). From north to south, we investigated seven study sites: Howe Island, West Dock, Deadhorse, Franklin Bluffs, Sagwon MNT (moist non-acidic tundra), Sagwon MAT (moist acidic tundra), and Happy Valley. The distance from

the coast to the site farthest south (Happy Valley) is about 130 km. Howe Island, West Dock, Deadhorse and Franklin Bluffs are located in the Arctic Coastal Plain, with abundant thaw lakes dotting the landscape. The remaining sites are situated in the Arctic Foothills, where the landscape is dominated by broad sloping valleys with elevations up to 350 m. The climate of the area varies with distance from the Arctic Ocean and elevation. From north to south, temperature and precipitation increase. On the Arctic Coastal Plain, the mean annual precipitation ranges from 125-140 mm and 50% falls as snow. In the Arctic Foothills, mean annual precipitation ranges from 140-270 mm, with 40% falling as snow (Haugen, 1982).

According to the Circumpolar Arctic Vegetation Map (CAVM Team, 2003) and Walker (2000), West Dock and Howe Island are part of bioclimate subzone C or the hemiprostrate dwarf-shrub subzone, with mean July temperatures from 5-7 °C. Sagwon MNT, Franklin Bluffs and Deadhorse are classified as bioclimate subzone D or the erect dwarf-shrub subzone, with mean July temperatures from 7-9 °C. Happy Valley and Sagwon MAT belong to bioclimate subzone E or the low-shrub subzone, with mean July temperatures from 9-12 °C.

Geology and soils

Howe Island, West Dock, Deadhorse and Franklin Bluffs are on the Arctic Coastal Plain, which was not glaciated during the last glaciation. It consists of alluvium and the surface is covered by predominately Holocene loess and organic deposits (Hamilton, 1987). The area shows several periglacial features, such as pingos, ice-wedge

polygons and nonsorted circles. Calcareous sediments are carried from limestone deposits at the headwaters of the Sagavanirktok River and redistributed as loess deposits on the coastal plain (Walker and Everett, 1991). Wet soils are often covered with marl due to the carbonate-rich parent material (Ping *et al.*, 1998). The Sagwon sites are about 100 km inland on the uplands at the northern edge of the Arctic Foothills. These sites have a loess mantle over Tertiary outwash consisting of rounded gravel. Happy Valley is on a glaciated surface mapped by Hamilton (1987) as Anaktuvuk-age (early Pleistocene) till. A thin layer of loess covers the till.

All sites are located in the zone of continuous permafrost (Péwé, 1975). The permafrost-affected soils, or cryosols, are in the Gelisol order of the U.S. Soil Taxonomy (Soil Survey Staff, 1999), and they contain permafrost within 1 m of the soil surface (Bockheim *et al.*, 1997). The soils show strong signs of soil mixing due to cryoturbation activity. The permafrost also acts as barrier for water percolation and leads to water-logged soils in spite of low precipitation, especially on the flat Arctic Coastal Plain. The high soil moisture content and cold soil temperatures result in slow decomposition rates, the accumulation of thick peat and gleyed soil horizons. Parts of the organic matter are often cryoturbated into lower parts of the active layer and can become locked up in the permafrost with changing environmental conditions (Ping *et al.*, 1998). The chemical soil properties change along the north-south climatic gradient and with distance from the Sagavanirktok River. The northern study sites exhibit soils with high pH and free carbonates. As the Arctic Foothills rise south from the Arctic Coastal Plain, the soils

become better drained with thinner loess deposits. Higher precipitation and greater leaching result in acidic soil reaction (Ping *et al.*, 1998).

METHODS

Field and laboratory methods

We established a total of 117 permanent plots along the bioclimate gradient, 15 at Howe Island, 5 at West Dock, 15 at Deadhorse, 37 at Franklin Bluffs, 15 at Sagwon MNT, 10 at Sagwon MAT and 20 at Happy Valley. Vegetation sampling was conducted during the summer periods of 2000 through 2003 using the centralized replicate sampling procedure (Mueller-Dombois and Ellenberg, 1974). We chose the plot, or relevé, locations subjectively in areas of homogeneous vegetation that were representative of the major plant communities. The minimum sampling area was 1 m^2 per plot. We used the Braun-Blanquet cover-abundance scale to score the cover of each species (Westhoff and van der Maarel, 1978). In addition, we recorded the cover of plant functional types and the average vegetation height. Nomenclature followed the PLANTS database (USDA NRCS, 2004) for vascular plants, Ignatov and Afonina (1992) for mosses, Esslinger (1997) for lichens and Konstantinova *et al.* (1992) for liverworts.

At each relevé, we recorded the following site information: percent bare soil, percent salt crust, cover of standing water, site moisture, glacial history, topography, site stability and elevation. We measured maximum snow depths in mid April 2002 to 2004, and maximum thaw depths in late August 2002 to 2004 using a metal probe. We correlated the vegetation information with the summer warmth index (SWI) calculated

for all study sites by Walker *et al.* (2004). The SWI is the sum of the monthly mean air temperatures above freezing and represents an integrated value for the total amount of summer warmth available for plant growth. We examined the change in morphology of frost-heave features along the bioclimate gradient by mapping several representative nonsorted circles at selected study sites at a 1 m by 1 m scale.

At each relevé site, we measured the depth of the organic horizon and collected soil samples of the upper 10 cm of the mineral horizon, which represents the rooting zone for most tundra species. All soil samples were shipped to the University of Alaska Fairbanks Palmer Soil and Plant Analysis Laboratory for analysis. Bulk density and volumetric soil moisture were calculated by drying field samples at 105 °C for 72 hours and determining percentage weight loss. All other analyses were completed on air-dried samples. Particle size was determined using the hydrometer method, taking readings at 40 seconds and 2 hours (Gee and Bauder, 1986). Soil pH values were measured using the saturated paste method with a glass electrode pH meter (Jackson, 1958). Total carbon and nitrogen were determined by dry combustion using a LECO CNS 2000 analyzer at 1350 °C (Robertson *et al.*, 1999). The availability of cations (K^+, Na^+, Ca^{2+}, Mg^{2+}) was determined with Mehlich-3 extractions (Mehlich, 1984).

Classification and ordination

We classified the vegetation according to the Braun-Blanquet sorted-table method (Mueller-Dombois and Ellenberg, 1974; Westhoff and van der Maarel, 1978) and the protocol suggested by Dierschke (1994) for distinguishing vegetation types. The relevés

were arranged in phytosociological tables to differentiate and characterize associations and community types. We placed the 117 relevés into preliminary groups based on climatic subzone, disturbance through frost action, soil pH and soil moisture content. We determined differential species and assessed the degree of fidelity of character species according to the criteria proposed by Dierschke (1994). The nomenclature of the described syntaxa is in accordance with the international code of phytosociological nomenclature (Weber *et al.*, 2000).

Detrended Correspondence Analysis (DCA) ordinations were carried out to analyze relationships between variation in vegetation and variation in environmental variables. We used PC-ORD (4.10 for Windows) (McCune and Mefford, 1999), and rare species were down-weighted and axes were rescaled based on program defaults. DCA produces first axes showing major directions of variation in the data and revealing the relationship of plant assemblages to major environmental gradients (Peet *et al.*, 1988). To evaluate the effectiveness of the ordination, we calculated an after-the-fact coefficient to determine the variance in the main matrix explained by DCA as suggested by McCune and Mefford (1999). The ordination axes are best described as complex environmental gradients with interrelated factors (Kent and Coker, 1992). Biplot diagrams were used to show the direction in the ordination diagram that has the maximum correlation with a particular environmental variable. DCA ordinations were compared with other ordination techniques available in PC-ORD (e.g. Bray-Curtis, Canonical Correspondence Analysis, Non-metric Multidimensional Scaling) using the same data set. We chose DCA as it produced results most consistent with the classification and showed strong underlying

environmental gradients. An added advantage of DCA is that the output also records the length of each axis in units of the average standard deviation of species turnover (SD units), which are a measure of species turnover (beta diversity) along the axis.

Plant functional types and floristic analysis

We analyzed growth form distributions (dwarf shrubs, forbs, graminoids, mosses, lichens and liverworts) and the floristic affinities of the communities. For the latter we used a multiple-character approach modified from the criteria by Walker (1985). Each vascular species was assigned to a class according to three categories: major regional unit (coastal, arctic, arctic-alpine, arctic-boreal), northern limits of plant distributions within the four climatic zones developed by Young (1971), and geographic range (North America, North America-Asia, North America-Asia-Europe, circumpolar). Young (1971) differentiated the climatic zones based on the sum of mean monthly temperatures above 0 °C (zone 1 = 0-6 °C, zone 2 = 6-12 °C, zone 3 = 12-20 °C, zone 4 = 20-35 °C). Zone 1 corresponds approximately to bioclimate subzone A, zone 2 to bioclimate subzones B and C, zone 3 to bioclimate subzone D, and zone 4 to bioclimate subzone E.

RESULTS AND DISCUSSION

Environmental and morphological characteristics

Frost-heave features differ from the surrounding tundra in several environmental characteristics. They have more bare ground than the adjacent tundra plots, and the percent of bare soil of the frost-heave features declines along the bioclimate gradient

from 55% in subzone C to 11% in subzone E (Table 2.1). At all sites, nonsorted circles and earth hummocks have greater thaw depths in late summer than the surrounding tundra. The difference in thaw depths between frost-heave features and tundra in subzone C averages about 14 cm and increases toward the south to 23 cm in subzone D and 27 cm in subzone E. The thick carpets of *Sphagnum* mosses apparently insulate the stable tundra in subzone E and reduce thaw depths. The study sites are located along a strong climatic gradient, with the SWI ranging from 9.3°C mo at Howe Island in subzone C to 30.2°C mo at Happy Valley in subzone E (Table 2.2). In the northern sites, the harsh climate prevents the soil of well-vegetated sites from thawing deeply. In the southern sites, biological constraints decrease thawing processes due to insulation by thick vegetation mats and organic horizons. Thus, the deepest thaw depths (mean 88 cm) are found at the nonsorted circles in subzone D. Average snow depths increase along the climate gradient from north to south from 19 to 63 cm (Table 2.1), probably due to increased precipitation associated with higher elevation (Ping and Moore, 1993). Also, stronger winds near the coast compact the snow, and much of the snow is lost due to ablation. The frost-heave features accumulate less snow than the adjacent tundra due to their raised soil surface caused by frost heave. Thinner snow cover should result in less insulated soils in the winter.

We found nonsorted circles dominating the landscape at Howe Island in subzone C (Fig. 2.2), periodically dotting the landscape in subzone D (Fig. 2.3) and being rather sporadic and inconspicuous in subzone E (Fig. 2.4). The morphological changes of nonsorted circles along the bioclimate gradient are shown in representative 1 m by 1 m

maps in Fig. 2.5. The nonsorted circles at Howe Island at the northern end of the bioclimate gradient are large in size and exhibit high cover of bare soil. Several contraction cracks dissect the nonsorted circles and form small contraction-crack polygons. The outer parts of the nonsorted circles are covered with lichen crusts. Further south in subzone D, the nonsorted circles have less amounts of bare soil and lichen crusts, and they are encircled by a thin vegetation mat growing inward from the edges of the nonsorted circles. Fewer contraction cracks are visible. The nonsorted circles and earth hummocks at Happy Valley at the southern end of the bioclimate gradient are fully vegetated and do not show any bare soil patches.

Classification

The classification of cryoturbated tundra in the Low Arctic of Alaska resulted in five associations and four community types that have been tentatively placed into four classes (Table 2.3). The dry nonacidic nonsorted circles and small contraction-crack polygons of subzone C (*Braya purpurascens-Puccinellia angustata* community) could not be placed into an actually described class. The following descriptions of the vegetation types are arranged according to climatic subzones, starting with the sites farthest north. Within each subzone, the vegetation types are sorted by soil moisture. Drier sites, usually disturbed through cryoturbation activity, are mentioned first.

Three plant communities are placed in the class Carici rupestris-Kobresietea bellardii Ohba 1974. This class includes mostly meso- to xerophytic, minerotrophic dwarf shrub and grass heath communities comprised of circumpolar arctic and alpine

species. The communities belong to the order Kobresio-Dryadetalia (Br.-Bl. 1948) Ohba 1974 and the North-American alliance Dryadion integrifoliae Ohba ex Daniëls 1982. The *Dryas integrifolia-Salix arctica* community belongs to the typical suballiance of the Dryadion integrifoliae. The Junco biglumis-Dryadetum integrifoliae and the Dryado integrifoliae-Caricetum bigelowii belong to the Dryadion integrifoliae suball. rhododendrenion lapponici, a new meso-hygrophytic suballiance described from Greenland by Lünterbusch and Daniëls (2004).

The moist coastal tundra of subzone C (Salici rotundifoliae-Caricetum aquatilis) and the wet nonacidic tundra of subzone D (*Scorpidium scorpioides-Carex aquatilis* community) are placed in the mire class Scheuchzerio-Caricetea nigrae (Nordh. 1936) Tx. 1937, order Scheuchzerietalia palustris Nordh. 1936, alliance Caricion lasiocarpae Vanden Berghen ap. Lebrun et al. 1949. This alliance includes wet basiphytic sedge beds on calcareous, poorly drained soils and occurs in the northern boreal zone and the Arctic.

The dry acidic nonsorted circles and earth hummocks (Cladino-Vaccinietum vitis-idaeae ass. nov.) as well as the moist acidic tundra (Sphagno-Eriophoretum vaginati Walker et al. 1994) of subzone E are placed in the class Loiseleurio-Vaccinietea Eggler 1952, order Rhododendro-Vaccinietalia Br.-Bl. ap. Br.-Bl. & Jenny 1926. This class includes dwarf shrub vegetation rich in lichens on acidic soil in alpine and arctic regions. We place the two associations provisionally within the alliance Loiseleurio-Diapension (Br.-Bl. et al. 1939) Daniëls 1982; however, the alliance position has yet to be determined.

The small, relatively wet acidic nonsorted circles of subzone E (*Anthelia juratzkana-Juncus biglumis* community) were placed within the snow patch class Salicetea herbaceae Br.-Bl. 1947, order Salicetalia herbaceae Br.-Bl. 1926, alliance Saxifrago-Ranunculion nivalis Nordh. 1943 emend. Dierß. 1984, suballiance Luzulenion arcticae (Nordh. 1936) Gjaerevoll 1950. The class comprises alpine and arctic snow-patch communities, which often exhibit solifluction and cryoturbation features, and the alliance is tied to arctic regions with relatively wet permafrost soils. The Luzulenion arcticae includes communities with arctic species on slightly drier soils.

Subzone C

***Braya purpurascens-Puccinellia angustata* community** (Fig. 2.6; Table 2.4; Appendix 2.1, ref. 1)

This community is found on the dry, nonacidic frost-heave features of subzone C, which are comprised of contraction-crack polygons and nonsorted circles. The small, nonsorted contraction-crack polygons, formed by desiccation and frost cracking, are up to 40 cm in diameter and form concentric rings around nonsorted circles measuring approximately 4 m in diameter (Fig. 2.7). These large frost-heave features, separated by thin strips of surrounding tundra vegetation, dominate the landscape. Cryoturbation activity is greatest at the center of the nonsorted circles, where bare mineral soil is exposed and small pebbles are heaved to the surface. The small contraction-crack polygons surrounding the nonsorted circles exhibit a thick crustose lichen cover and are

more stabilized. Several small islands within and near the delta of the Sagavanirktok River exhibit these conspicuous frost-heave features. Subzone C represents only a small band along the northern coast in Alaska; thus, this community is not very common in Alaska. However, counterparts are found in the Middle Arctic (sensu Polunin, 1951) in Canada and have been described from Green Cabin on Banks Island (Walker *et al.*, unpublished data).

We could not place this community into an existing class. The soils show a high Na^+ content due to the input of ocean spray. This agrees with Michaelson *et al.* (2005), who found differences in salt species and their distribution and accumulation patterns in nonsorted circles and tundra plots in the Alaskan Arctic tundra. Na^+ affected the bare microsites on coastal sites and caused smooth crusts due to soil dispersion. The vascular species of this community are all halophytic or salt tolerant, such as *Braya glabella* ssp. *purpurascens* and *Puccinellia angustata*. This suggests similarities to Type B10 Dry *Braya purpurascens-Puccinellia andersonii* forb grass barren of the coastal bluffs in the Prudhoe Bay area described by (1985). The community also shows some affinities to crustose lichen-dominated plant communities at Prudhoe Bay, Types B1, B2, B3 (Walker, 1985), where *Lecanora epibryon* is often dominant on mineral soils. The community shares some floristic elements with the *Puccinellia* stands of arctic coastal salt meadows described by Thannheiser (1991), although the *Braya purpurascens-Puccinellia angustata* community does not exhibit a continuous vegetation cover.

The soils are classified as Aquic Haploturbels (Michaelson *et al.*, 2005). An organic horizon is absent, and the exposed mineral soil shows signs of desiccation

cracking and/or seasonal frost cracking (Washburn, 1980). The mineral soil is light brownish gray and has a sandy loam texture. Soil moisture is very low (mean 28%, Table 2.1), and the soil pH is high (mean 8.3). The sparse vegetation cover acts as a poor insulator and allows for deep thaw depth (mean 79 cm). Maximum snow depth is shallow (mean 8 cm) due to the proximity to the coast.

The community is separated into two variants; the first occurs on barren nonsorted circles and the second occurs on the small contraction-crack polygons. The *Braya purpurascens-Puccinellia angustata* community typical variant is very poor in species, the only constant taxa being *Braya glabella* ssp. *purpurascens*, *Puccinellia angustata* and *Polyblastia sendtneri*. *Braya glabella* ssp. *purpurascens* and *Puccinellia angustata* are faithful. The small contraction-crack polygons feature the *Mycobilimbia lobulata* variant, which is richer in species, especially nonvascular species. A thick lichen crust consisting of *Fulgensia bracteata*, *Lecanora epibryon*, *Mycobilimbia lobulata*, *Polyblastia bryophila* and *P. sendtneri* covers the small contraction-crack polygons. The *Mycobilimbia lobulata* variant shares several taxa with the nearby *Dryas integrifolia-Salix arctica* community, including *Cerastium beeringianum*, *Chrysanthemum integrifolium* and *Salix ovalifolia*. These species are more abundant in the *Dryas integrifolia-Salix arctica* community and seem to slowly invade the edges of the contraction-crack polygons from the surrounding tundra areas.

***Dryas integrifolia-Salix arctica* community** (Fig. 2.8; Table 2.5; Appendix 2.1, ref. 2)

This community is confined to the cracks and depressions between the large frost-heave features in subzone C. The community is not widely distributed in Alaska because subzone C covers only a narrow belt close to the Beaufort Sea. We found the community on islands close to the shore of the Beaufort Sea and nearby the delta of the Sagavanirktok River. It also appears to be invading the more stabilized small contraction-crack polygons of the *Braya purpurascens-Puccinellia angustata* community. In the summer, geese nest on the islands close to the shore and have a major impact on the vegetation due to feeding on plants and excreting nitrogen-rich feces. The community is closely related to Type B2 Dry *Dryas integrifolia-Saxifraga oppositifolia-Lecanora epibryon* dwarf-shrub, crustose-lichen tundra (Walker, 1985). The community is similar to the cushion plant communities described from the Canadian High Arctic polar semi-deserts by Bliss *et al.* (1984), which are dominated by *Dryas integrifolia*, *Salix arctica* and *Saxifraga oppositifolia* and, unlike the community described here, are poor in bryophytes.

The soils are Aquic Haploturbels and very similar to the ones associated with the *Braya purpurascens-Puccinellia angustata* community. The organic horizon is thin (0.5 cm, Table 2.1) and peaty. The mineral soil is grayish brown and consists of fine sandy loam. Soil moisture is low (mean 37%) and the pH averages 7.9. Although this community is not associated with differential frost-heave features, maximum thaw depth is deep (mean 65 cm) due to the thin vegetation cover. Maximum snow depth averages 13 cm.

This community is relatively rich in vascular species. The dwarf shrubs *Dryas integrifolia*, *Salix arctica*, *S. ovalifolia* and *Saxifraga oppositifolia* and the mosses *Ctenidium procerrimum* and *Ditrichum flexicaule* dominate the community. Faithful taxa include *Chrysanthemum integrifolium*, *Festuca baffinensis*, *Salix ovalifolia* and *Ctenidium procerrimum.*

Salici rotundifoliae-Caricetum aquatilis Kade *et al.* ass. nov. (Fig. 2.9; Table 2.6, nomenclatural type relevé no. 98; Appendix 2.1, ref. 3)

The Salici rotundifoliae-Caricetum aquatilis occurs in a narrow belt of coastal circumneutral tundra in Northern Alaska. We placed this association in the class Scheuchzerio-Caricetea nigrae; however, the association is transitional to the plant communities of the Dryadion integrifoliae with regards to species composition. We found this association near West Dock at Prudhoe Bay on thin eolian silts and sands that overlie alluvial gravels of the ancient Sagavanirktok River flood plain. The coarse gravels inhibit frost heave to a large extent, and nonsorted circles were not present because of the thick gravel deposits close to the surface. The landscape is characterized by flat- and low-centered polygons with diameters of 10-15 m. Standing water can occur in spring or after heavy rain. Thick coastal fog during the summer and fall is typical.

Yurtsev (1994) placed the coastal tundra vegetation from the Cape Barrow-Prudhoe Bay area along with the eastern coast of Central Chukotka into the southern subdivision of the arctic tundra subregion and characterized the vegetation by extensive peaty wet meadows, the occasional occurrence of hypoarctic ericaceous dwarf shrub

species and very low species diversity, reflecting the "youthfulness" of this type of arctic tundra. The Salici rotundifoliae-Caricetum aquatilis is equivalent to the moist to wet coastal tundra of polygon centers in the Prudhoe Bay area (Type U12 Moist *Carex aquatilis, Salix planifolia* ssp. *pulchra, Campylium stellatum* sedge, dwarf-shrub tundra) recorded by Walker (1985) and to the moist *Carex aquatilis-Oncophorus wahlenbergii* meadow in the Point Barrow area, Alaska, recorded by Webber (1978). Elias *et al.* (1996) described a *Dryas integrifolia-Carex aquatilis* community type on moist nonacidic coastal sites at Barter Island and a *Saxifraga cernua-Carex aquatilis* community type on more acidic flat-centered polygons, moist meadows and areas with moderate drainage from Point Barrow, Alaska. The *Saxifraga cernua-Carex aquatilis* community is most similar to that at West Dock and is dominated by *Alopecurus alpinus, Carex aquatilis, Dupontia fisheri, Eriophorum angustifolium, Petasites frigidus, Saxifraga cernua* and *Oncophorus wahlenbergii.*

The soils of the polygon centers are classified as Typic Historthels (Ping *et al.*, 1998). The soils are relatively poorly drained, and standing water is sometimes present early in the summer and during rainy periods. Saturation, due to relatively high soil moisture (mean 47%, Table 2.1), reduces decomposition, resulting in thick organic horizons (mean 27 cm). The mineral horizon is dark gray and gleyed. Soil texture is loam. Although part of the nonacidic tundra, the soils of this association have a relatively low pH (mean 6.5) when compared to other areas of the Prudhoe Bay region. This might be due to the coastal influence. Winds directly from the Beaufort Sea reduce the input of calcareous loess from the Sagavanirktok River delta (Walker, 1985). Maximum thaw

depth is shallow (mean 28 cm). The sites receive only small amounts of snow (mean 19 cm).

This sedge tundra is relatively rich in species, especially in nonvascular taxa. The association is generally dominated by *Carex aquatilis.* Other constant taxa are *Dryas integrifolia, Eriophorum angustifolium* ssp. *triste, Salix arctica, S. rotundifolia, Cetraria islandica, Dactylina arctica* and *Thamnolia subuliformis.* Faithful taxa include *Poa arctica, Salix rotundifolia, Cladonia pyxidata* and *Nephroma expallidum.*

Subzone D

Junco biglumis-Dryadetum integrifoliae Kade *et al.* ass. nov. (Table 2.7, nomenclatural type relevé no. 106; Appendix 2.1, ref. 4)

The Junco biglumis-Dryadetum integrifoliae is associated with nonsorted circles within the moist nonacidic tundra of subzone D. The association has floristic affinities to the fellfield-like *Carex rupestris-Saxifraga oppositifolia* community type of dry, exposed, east- and north-facing slopes of pingos of the Alaskan Arctic Coastal Plain (Walker *et al.*, 1991). Walker *et al.* (1991) likened this group to fellfield vegetation because of its abundance of cushion and mat-forming plants and crustose lichens. Gelting (1955) described closely related *Dryas integrifolia* communities from western Greenland on basalt rich soils, which are rich in crustose lichens such as *Lecanora epibryon, Ochrolechia upsaliensis* and *Pertusaria panyrga.* Chernov and Matveyeva (1997) recognized the vegetation occurring on frost scars as a separate stage in the successional formation of zonal tundra on the Taymyr Peninsula, Russia. They distinguished between

several elements at this successional stage: patches of bare ground with solitary plants (which corresponds to this community type), rims with grass/dwarf-shrub/moss turf and troughs with moss turf. The process of bare-ground overgrowth is in its early stages, with an organogenic crust forming and stabilizing the ground. The thin crust is part of a micro-successional cycle, being periodically destroyed trough frost action and reestablishing itself. However, Chernov and Matveyeva (1997) viewed the vegetation growing on frost scars as part of a "spotted tundra" complex and did not describe it as a separate plant-community type.

The soil types of this association vary with site moisture conditions. Aquic Haploturbels are found on drier sites and Typic Aquiturbels on moist to wet sites (Michaelson *et al.*, 2005). Organic horizons are very thin (0.2 cm, Table 2.1). The mineral soil is dark yellowish brown and has a loam texture. Soil moisture is relatively low (mean 39%), but soils can exhibit gleyed characteristics where site moisture is locally greater. The soil pH is high (mean 8.1). The thin vegetation mat and organic horizons allow for great thaw depth (mean 88 cm). Maximum snow depth is shallow and averages 27 cm.

Taxa faithful for this association are *Carex capillaris*, *Senecio resedifolius*, *Aneura pinguis*, *Bryum wrightii*, *Cladonia pocillum* and *Solorina bispora*. Other dominant taxa are *Dryas integrifolia*, *Eriophorum angustifolium* ssp. *triste*, *Saxifraga oppositifolia*, *Ditrichum flexicaule*, *Hypnum bambergeri*, *Polyblastia sendtneri* and *Thamnolia subuliformis*.

This association has several species in common with the dry nonacidic tundra and nonsorted circles of subzone C, such as *Encalypta* sp., *Lecanora epibryon*, *Leiocolea collaris*, *Polyblastia sendtneri* and *Rinodina roscida*. It seems that the nonsorted circles in subzone D might serve as "islands" for certain species occurring in communities farther north. The disturbance through frost action creates habitat conditions similar to the physically harsh ones that are more common farther north, such as dry exposed mineral soil with greater temperature fluctuations at the surface due to the lack of insulation. Under the more favorable climatic conditions of subzone D, species occurring on these relatively rare sites would otherwise be outcompeted by species occurring in the adjacent tundra.

The association is divided into two subassociations based on cryoturbation activity and plant abundance. The Junco biglumis-Dryadetum integrifoliae typicum is found on active, barren nonsorted circles. The Junco biglumis-Dryadetum integrifoliae pedicularetosum occurs on stabilized nonsorted circles with greater plant covers.

Junco biglumis-Dryadetum integrifoliae typicum subass. nov. (Fig. 2.10; Table 2.7, nomenclatural type relevé no. 106)

The Junco biglumis-Dryadetum integrifoliae typicum occurs on barren nonsorted circles within moist nonacidic tundra. The association colonizes nonsorted circles that show great cryoturbation activity. Up to 50% of the soil surface is barren, and the soil commonly exhibits a "cottage cheese" structure as a result of diurnal needle-ice

formation during the early summer. The association establishes itself mainly in small desiccation cracks of the nonsorted circles, where site conditions are more favorable, and expands further from there. We found this subassociation under a variety of topographic positions and soil moisture conditions. The Junco biglumis-Dryadetum integrifoliae typicum is equivalent to the Type B3 Dry *Saxifraga oppositifolia, Juncus biglumis* forb barrens (Walker, 1985) occurring on frost scars in the Prudhoe Bay vicinity, Alaska. Walker (1985) mentions *Dryas integrifolia, Juncus biglumis, Minuartia arctica, Saxifraga oppositifolia, Bryum wrightii* and *Lecanora epibryon* as distinct taxa occurring on the dry, barren features.

The subassociation is dominated by the black crustose lichen *Polyblastia sendtneri.* At our study plots, this species is restricted to plant communities affected by soil-surface disturbance, such as the frost-heave community *Braya purpurascens-Puccinellia angustata* and the Junco biglumis-Dryadetum integrifoliae. In addition, *Eriophorum angustifolium* ssp. *subarcticum* and *Juncus triglumis* occur in areas with high soil moisture.

Junco biglumis-Dryadetum integrifoliae pedicularetosum subass. nov.

(Fig. 2.11; Table 2.7, nomenclatural type relevé no. 32)

The Junco biglumis-Dryadetum integrifoliae pedicularetosum is associated with stabilized nonsorted circles in the moist nonacidic tundra. The nonsorted circles are well vegetated and may exhibit just a small central area of active soil churning. This subassociation represents a mid- to late-successional stage on the nonsorted circles:

It invades the edges of active nonsorted circles that support the Junco biglumis-Dryadetum integrifoliae typicum in the center parts (see above), and it is dominant on less active nonsorted circles, reducing cryoturbation activity through insulation and shading. It is more or less equivalent to the Type B2 Dry *Dryas integrifolia-Saxifraga oppositifolia-Lecanora epibryon* dwarf shrub, crustose lichen tundra described from Prudhoe Bay (Walker, 1985), which occurs on frost-disturbed sites. The subassociation is also very similar to the *Ochrolechia frigida-Dryas integrifolia* community type of the dry sites on Barter Island, Alaska described by Elias *et al.* (1996). This community type is dominated by *Dryas integrifolia* and a suite of fruticose lichens and occurs on base-rich mineral soils that are cryoturbated.

This subassociation is richer in vascular plant taxa than the Junco biglumis-Dryadetum integrifoliae typicum. Differential taxa against it include *Arctostaphylos rubra*, *Minuartia arctica*, *Pedicularis kanei*, *Senecio atropurpureus*, *Dactylina arctica* and *Tomentypnum nitens*. Most of these species are also common to the surrounding Dryado integrifoliae-Caricetum bigelowii of the moist nonacidic tundra of subzone D (see below), confirming that this subassociation represents a successional stage between the barren nonsorted circles associated with the Junco biglumis-Dryadetum integrifoliae typicum and the Dryado integrifoliae-Caricetum bigelowii of the stable tundra. This subassociation also differs morphologically from the typicum, with *Dryas integrifolia*, *Eriophorum angustifolium* ssp. *triste*, *Ditrichum flexicaule*, *Flavocetraria cucullata*, *Hypnum bambergeri* and *Thamnolia subuliformis* having distinctly greater cover abundance scores.

Dryado integrifoliae-Caricetum bigelowii Walker *et al.* 1994 (Fig. 2.12; Table 2.8; Appendix 2.1, ref. 5)

Walker *et al.* (1994) described this association as the "non-acidic counterpart to the Sphagno-Eriophoretum vaginati, occurring on circumneutral mesic uplands and hillslopes, and limited to younger landscapes". They placed the association within the mire and fen class Scheuchzerio-Caricetea nigrae, which includes basiphytic, moss-rich communities on poorly drained soils. However, we feel this association should rather be placed within the alliance Dryadion integrifoliae Ohba ex Daniëls 1982, class Carici rupestris-Kobresietea bellardii Ohba 1974, which includes dwarf shrub and grass heath communities. The Dryado integrifoliae-Caricetum bigelowii includes the Type U3 Moist *Eriophorum triste-Dryas integrifolia* sedge, dwarf-shrub tundra described from the Prudhoe Bay area by Walker (1985). He found the community type on mesic upland sites, tops of poorly developed high-centered polygons and strangs in wetter areas. He described the community type as rich in sedges (*Carex aquatilis*, *C. bigelowii*, *C. membranacea*, *Eriophorum angustifolium* ssp. *triste*) and dwarf-shrubs (*Dryas integrifolia*, *Salix arctica*, *S. reticulata*). The *Dryas integrifolia-Carex aquatilis* community type mentioned by Elias *et al.* (1996) is very similar in species composition and represents the most common vegetation on moist sites on Barter Island, Alaska. On the dry, exposed slopes of the Brooks Range, Alaska, the Caricetum scirpoideo-rupestris (Cooper, 1986) has a similar species composition, with *Dryas octopetala* ssp. *octopetala* replacing *Dryas integrifolia*. Cooper (1986) mentions the similarity of this *Dryas*-stand type to vegetation described from Montana and eastern Canada. In addition,

the *Dryas octopetala*-communities described from Spitsbergen (Rønning, 1964; Hartmann, 1980) represent close allies. When occurring on moist to wet soils, the Dryado integrifoliae-Caricetum bigelowii is also closely allied with the *Eriophorum angustifolium-Rhododendron lapponicum* community, a fen vegetation on wet soils described from Greenland by Lünterbusch and Daniëls (2004). Another close ally is the Carici arctisibiricae-Hylocomietum alaskani described by Matveyeva (1994) from the Taimyr Peninsula in Russia, where *Dryas punctata* replaces *Dryas integrifolia*. It seems that most *Dryas*-dominated vegetation stands occur on moist to dry, circumneutral substrates under continental climatic regimes (but see Lünterbusch and Daniëls (2004) for *Dryas* communities on moist to wet soil). We found this association widely distributed on stable soils on mid slopes and hilltops in the moist nonacidic tundra of subzone D. These areas receive loess depositions from the Sagavanirktok River and favor the development of minerotrophic plant communities (Walker and Everett, 1991). Nonsorted circles associated with either the Junco biglumis-Dryadetum integrifoliae or the Saxifrago oppositifoliae-Dryadetum integrifoliae represent common breaks in the association.

Similar to the Saxifrago oppositifoliae-Dryadetum integrifoliae, the soils are classified as Aquic Haploturbels on drier sites and Aquic Ochreturbels on moist sites (Michaelson *et al.*, 2005). The organic horizons are well-developed (15 cm, Table 2.1) as a dark brown peaty muck. The mineral horizons often show signs of redox processes with mottled reddish dark brown and dark gray colors. Soil texture is loam, and soil moisture averages 45%. Mean soil pH is 7.9. The soils have relatively shallow thaw

depths and moderate snow depth when compared to the nonsorted circles that dot the area (means 65 cm and 40 cm, respectively).

Species richness is high in this association, averaging 43 species. *Arctostaphylos rubra*, *Carex bigelowii*, *Papaver macounii*, *Salix reticulata* and *Saussurea angustifolia* are faithful. The association is dominated by *Arctostaphylos rubra*, *Carex bigelowii*, *C. membranaceae*, *Dryas integrifolia*, *Eriophorum angustifolium* ssp. *triste*, *Salix arctica* and *S. reticulata*, *Ditrichum flexicaule*, *Hypnum bambergeri* and *Tomentypnum nitens*. Other constant taxa include *Cardamine hyperborea*, *Polygonum viviparum*, *Senecio atropurpureus*, *Cetraria islandica*, *Flavocetraria cucullata* and *Thamnolia subuliformis*.

The association is differentiated into three variants along the climate gradient, with mean species richness increasing from 35 to 55 species from north to south. Towards the north of subzone D at Deadhorse, the *Eriophorum angustifolium* ssp. *subarcticum* variant is found in wetter environments on level ground. Differential vascular taxa are *Eriophorum angustifolium* ssp. *subarcticum*, *Pedicularis sudetica* ssp. *albolabiata* and *Saxifraga oppositifolia*. The moss cover shows great species variety and includes numerous hygrophytic species, with *Campylium stellatum*, *Catoscopium nigritum*, *Drepanocladus brevifolius* and *Orthothecium chryseum* being differential. The *Carex scirpoidea* variant occurs in the Franklin Bluffs area on moist soils. Differential taxa include *Carex scirpoidea*, *Bryum pseudotriquetrum* and *Cladonia pocillum*. The *Lupinus arcticus* variant is found towards the warmer, southern end of subzone D on relatively well-drained slopes in the Sagwon Hills. This variant is especially rich in vascular taxa. Differential taxa include *Equisetum arvense*, *Lupinus arcticus*, *Saxifraga*

hieracifolia, Aulacomnium turgidum, Dicranum spadiceum, Hylocomium splendens and *Rhytidium rugosum.*

***Scorpidium scorpioides-Carex aquatilis* community** (Fig. 2.13; Table 2.9; Appendix 2.1, ref. 6)

This wet sedge community is associated with poorly drained soils in the nonacidic tundra of subzone D. The areas usually have standing water early in the summer, and the soil surface is commonly covered with marl deposits. Almost barren nonsorted circles with thick marl deposits interrupt the otherwise closed sedge canopy. This community occurs on wetter soils than the Salici rotundifoliae-Caricetum aquatilis or the *Eriophorum angustifolium* ssp. *subarcticum* variant of the Dryado integrifoliae-Caricetum bigelowii described above. Walker and Everett (1991) described a similar wet sedge-community type from the Prudhoe Bay area (wet *Carex aquatilis-Scorpidium scorpioides* sedge tundra, Type M4 in Walker, 1985), where it occurs in basins, troughs of low-centered polygons and lake margins with soil pH values above 7. They considered this community to be a transitional type between the wet and the aquatic tundra types, as it has up to 10 cm of standing water throughout the summer. This community also shows similarities to the *Eriophorum angustifolium-Carex aquatilis* community type described from hygric nonacidic fens in the Arctic Foothills of Alaska by Walker *et al.* (1994), and described from wet meadows and the basins of low-centered polygons with saturated soils at Point Barrow and Barter Island, Alaska, by Elias *et al.* (1996). The community is

allied with the Paludello squarrosae-Caricetum aquatilis described from the fens and marshes of the valley bottoms of the Brooks Range, Alaska, by Cooper (1986).

The soils are Typic Historthels (Ping, pers. comm.) and remain water-saturated throughout the summer. The anaerobic conditions result in thick, black, mucky organic horizons (25 cm, Table 2.1) due to slow decomposition rates. The upper parts of the organic horizon are often less decomposed and show recognizable plant parts in the peat. The mineral horizon is dark gray and gleyed, and soil texture is loam. Soil moisture is relatively high (mean 49%). Soil pH averages 7.7. The soils not disturbed by cryoturbation reach a mean maximum thaw depth of 70 cm. This thaw depth is slightly greater than at the drier tundra sites of the Dryado integrifoliae-Caricetum bigelowii, probably due to the fact that wet soils conduct heat better than drier soils. The sites receive a relatively great amount of snow (mean 59 cm) due to their topographic position (depressions and toe slopes).

This community is poor in species, especially in nonvascular taxa. *Eriophorum angustifolium* ssp. *subarcticum* reaches cover values of up to 75% and dominates the community. Faithful taxa are *P. sudetica* ssp. *albolabiata* and *Carex aquatilis*. Other constant taxa include *Equisetum variegatum*, *Salix arctica* and *Scorpidium scorpioides*.

Subzone E

Cladino-Vaccinietum vitis-idaeae Kade *et al.* ass. nov. (Fig. 2.14; Table 2.10, nomenclatural type relevé no. 91; Appendix 2.1, ref. 7)

This dwarf shrub-rich community is found on relatively dry to moist acidic nonsorted circles and earth hummocks on well-drained slopes and hilltops in subzone E. The nonsorted circles of this subzone are commonly overgrown with vegetation and exhibit only very small patches of bare soil. The earth hummocks show little cryoturbation activity as they are well insulated by the thick vegetation mat. The nonsorted circles and earth hummocks represent frequent breaks in the surrounding moist acidic tundra (Sphagno-Eriophoretum vaginati, see below). Relatively dry nonsorted circles associated with upper hill slope positions usually exhibit the Cladino-Vaccinietum vitis-idaeae; whereas wetter nonsorted circles occurring on toe slopes feature the *Anthelia juratzkana-Juncus biglumis* community (see below).

The Cladino-Vaccinietum vitis-idaeae is similar in species composition to the Sphagno-Eriophoretum vaginati covering the surrounding moist acidic tundra. Both associations are dominated by dwarf shrubs such as *Betula nana*, *Ledum palustre* ssp. *decumbens* and *Vaccinium vitis-idaea*. However, the Cladino-Vaccinietum vitis-idaeae does not support the growth of *Sphagnum* mosses, as it is associated with the drier soils of elevated earth hummocks and higher hill-slope positions and has abundant lichen cover. The association is allied with the Salici phlebophyllae-Arctoetum alpinae Walker *et al.* 1994, which occurs on well drained, moderately exposed, acidic rocky sites of the Arctic Foothills. It exhibits a high diversity of fruticose

lichens, such as *Cetraria cucullata, C. islandica, C. nivalis, Cladina arbuscula, C. rangiferina* and *C. uncialis*. Common dwarf shrubs include *Salix phlebophylla, Vaccinium uliginosum* and *V. vitis-idaea*. Cooper (1986) described two associations from the Arrigetch Creek Valley, Brooks Range, Alaska, which also show affinities to the Cladino-Vaccinietum vitis-idaeae. The Betulo glandulosae-Cladonietum stellaris Cooper 1986 occurs on relatively dry granitic glacial moraines and is dominated by *Cladonia* lichens. Here, *Betula glandulosa* replaces *Betula nana*, and both the Cladino-Vaccinietum vitis-idaeae and the Betulo glandulosae-Cladonietum stellaris have *Ledum palustre* ssp. *decumbens, Vaccinium vitis-idaea* and a variety of *Cladonia* species in common. The Vaccinio uliginosi-Salicetum phlebophyllae Cooper 1986 is a prostrate shrub vegetation type of windswept ridge tops on acidic mineral soils and is dominated by *Loiseleuria procumbens, Salix phlebophylla, Vaccinium uliginosum, V. vitis-idaea* and several "wind lichens" such as *Cetraria kamzaticum, Cornicularia divergens* and *Sphaerophorus globosus*. Dierßen (1996) combined several *Racomitrium lanuginosum* heath communities described from Iceland, Greenland, Norway and Scotland into the Carici bigelowii-Racomitrietum lanuginosi (Du Rietz 1925) Dahl 1957. *Racomitrium lanuginosum* reaches its optimal vitality in this association, but in contrast to the Cladino-Vaccinietum vitis-idaeae, vascular plants play only a minor role.

The soils are classified as Ruptic-Histic Aquiturbels (Ping *et al.*, 1998). The organic horizons range in thickness from 0 to 15 cm and consist of dark brown mucky peat. The mineral soil is yellowish brown to dark brown with clay loam texture. Soil

moisture is low (mean 36%, Table 2.1), and soil pH averages 5.0. Thaw depths of the nonsorted circles and hummocks average 60 cm and are shallower than the thaw depths of the more active frost-heave features in the northern subzones. Snow depth averages 40 cm.

This association is especially rich in nonvascular species; the following are faithful to this association: *Cladina arbuscula*, *Dicranum spadiceum*, *Polytrichum hyperboreum* and *Racomitrium lanuginosum*. The dominant taxa are *Betula nana*, *Cassiope tetragona*, *Empetrum nigrum* ssp. *hermaphroditum*, *Ledum palustre* ssp. *decumbens*, *Petasitis frigidus*, *Polygonum bistorta* var. *plumosum*, *Vaccinium vitis-idaea*, *Anastrophyllum minutum*, *Aulacomnium turgidum*, *Cladina rangiferina*, *Dicranum elongatum*, *Flavocetraria cucullata* and *Hylocomium splendens*. A variety of *Cladonia* and *Cladina* lichens play an important role in this association. Most species are shared with the surrounding Sphagno-Eriophoretum vaginati. However, the elevated, drier soils of the nonsorted circles and earth hummocks support a rich assortment of nonvascular species, which are differential against the Sphagno-Eriophoretum vaginati.

The association is split into two variants. The *Racomitrium lanuginosum* variant grows on flat nonsorted circles with more mineral-rich soils and moderate cryoturbation activity, and the *Carex bigelowii* variant is associated with raised, stabilized earth hummocks with more peaty soils. The *Racomitrium lanuginosum* variant is richer in nonvascular taxa and is dominated by a dense moss carpet of *Racomitrium lanuginosum*. Other differential taxa include *Arctagrostis latifolia*, *Senecio atropurpureus* and

Pertusaria dactylina. The *Carex bigelowii* variant is differentiated by *Carex bigelowii* and *Cetraria islandica*.

Sphagno-Eriophoretum vaginati Walker *et al.* 1994 (Fig. 2.15; Table 2.11; Appendix 2.1, ref. 8)

Walker *et al.* (1994) consider the Sphagno-Eriophoretum vaginati to be the zonal vegetation of the Arctic Foothills, Alaska. It is widespread on mesic, acidic soils of the upland tundra, covering gentle, poorly drained slopes. Although occurring on uplands, this association includes some hygrophytic species due to the high water-holding capacity of the *Sphagnum* mosses. Walker *et al.* (1994) placed the association within the bog and wet heaths class Oxycocco-Sphagnetea Br.-Bl. & Tx. 1943 ap. Westh. et al. 1946, which comprises dwarf shrub heaths and bogs on acidic, poorly drained substrates. However, the class Oxycocco-Sphagnetea has its main distribution in nemoral and boreal areas and is only weakly developed in the Arctic. We feel the Sphagno-Eriophoretum vaginati should rather be grouped in the class Loiseleurio-Vaccinietea Eggler 1952, which includes dwarf shrub vegetation on acidic soils in alpine and arctic regions.

The Sphagno-Eriophoretum vaginati is common in upland regions of northwestern Canada and northeastern Russia (Bliss and Matveyeva, 1992; Chernov and Matveyeva, 1997). It is the predominant association on the uplands in unglaciated tundra areas of Beringia with ice-rich permafrost. The association is dominant on the mesic slopes and hilltops of the acidic tundra in subzone E, commonly interspersed with large,

often inactive nonsorted circles and earth hummocks (Cladino-Vaccinietum vitis-idaeae). Not so common and restricted to slightly wetter areas are small and barren active nonsorted circles (*Anthelia juratzkana-Juncus biglumis* community, see below).

The soils are classified as Histic Aquiturbels (Ping *et al.*, 1998). Organic horizons are about 12 cm thick (Table 2.1) and consist of dark brown mucky peat. They overlay dark gray, gleyed mineral horizons with loam texture. In places with better drainage, mineral soils lack gleyed features and are dark yellowish brown. Soil moisture averages 44% and soil pH is low (mean 5.3). The soils are insulated by a deep *Sphagnum* moss cover and exhibit shallow thaw depths (mean 34 cm). Maximum snow depth averages 60 cm.

The association is rich in nonvascular taxa (mean 28 taxa) but relatively poor in vascular taxa, especially in comparison to the Dryado integrifoliae-Caricetum bigelowii (means 14 and 24 vascular species, respectively). Faithful taxa are *Pedicularis lapponica*, *Salix planifolia* ssp. *pulchra*, *Sphagnum angustifolium*, *S. girgensohnii* and *S. warnstorfii*. The abundant tussock-forming sedge *Eriophorum vaginatum* gives this vegetation type its characteristic look. Together with *Eriophorum vaginatum*, the dwarf shrubs *Betula nana*, *Cassiope tetragona*, *Empetrum nigrum*, *Ledum palustre* ssp. *decumbens*, *Salix planifolia* ssp. *pulchra* and *Vaccinium vitis-idaea* are dominant in the overstory. Thick moss mats of *Aulacomnium turgidum*, *Hylocomium splendens* and a variety of *Dicranum* and *Sphagnum* species are found in the small depressions next to the tussocks. This association shares many species with the

Cladino-Vaccinietum vitis-idaeae, with *Eriophorum vaginatum*, *Salix planifolia* ssp. *pulchra* and the *Sphagnum* mosses being differential against it.

***Anthelia juratzkana-Juncus biglumis* community** (Fig. 2.16; Table 2.12; Appendix 2.1, ref. 9)

Walker *et al.* (1994) described this unit occurring on nonsorted circles as a distinct community within the tussock tundra of the Alaskan North Slope. We found this community associated with small, active, barren nonsorted circles of the moist acidic tundra in subzone E. These nonsorted circles represent a rather inconspicuous component of the surrounding Sphagno-Eriophoretum vaginati. These small features, measuring only up to 40 cm in diameter, are restricted to the wetter inter-tussock sites and are common on toe slopes of hills at Happy Valley. They are usually placed 15 m or more apart and can be difficult to spot as they are sometimes hidden under *Eriophorum vaginatum* tussocks and dwarf-shrub branches.

The soils are classified as Typic Aquiturbels (Ping, pers. comm.). Organic horizons are absent, and the mineral soil surface is either bare or covered by a thin layer composed of cryptogamic liverworts, mosses and lichens that readily peels off the mineral soil. The mineral soils have very dark gray, gleyed horizons and a clay loam texture. Soil moisture content averages 42% (Table 2.1) and soil pH averages 5.2. The lack of a thick insulative vegetation mat or organic horizon results in deep thaw (mean 60 cm). The low position along the hill slope is responsible for snow accumulation, and maximum snow depth is rather deep, averaging 63 cm.

The community is dominated by nonvascular species. The nonvascular species composition of this community is similar to several moss synusia of snow patch communities compiled by Dierßen (1996). The leafy liverwort *Anthelia juratzkana* forms an almost continuous carpet on most of the nonsorted circles. Faithful taxa are *Cephalozia bicuspidata, Dicranella subulata* and *Jungermannia confertissima. Juncus biglumis* and *Luzula arctica* are also restricted to these barren areas. In addition, there are several constant taxa that are invading from the surrounding Sphagno-Eriophoretum vaginati: *Betula nana, Eriophorum vaginatum, Ledum palustre* ssp. *decumbens, Vaccinium vitis-idaea* and *Hylocomium splendens*. This community shares a few species with the associations occurring on nonacidic nonsorted circles, such as *Juncus biglumis, Dactylina ramulosa* and *Pohlia* sp.

Ordination

The DCA ordination diagram shows the relationship between plant communities and environmental variables (Fig. 2.17). The ordination axes show the major directions of variation in the data; the first axis explains 53% and the second axis explains 11% of the variation. The arrows within the biplot diagram display the principal direction of variation and strength of correlation for major environmental variables. Only environmental variables with $R^2 > 0.35$ are shown.

Axis 1 of the DCA ordination is interpreted as a more or less complex bioclimate/pH gradient, which corresponds to the south-to-north negative trend in temperature and positive trend in soil pH. Soil pH, thaw depth and the amount of bare

ground increase along axis 1, and air temperature as measured by the SWI, elevation, snow depth and cover of erect dwarf shrubs decrease along axis 1. Thaw depth increases along axis 1 along with decreasing vegetation cover, which allows the soil to warm up more in the summer. Snow depth increases towards the south with increasing elevation. Communities of subzone E occupy the left end of the gradient and communities of subzone C the right end. The coastal tundra plots at West Dock are an exception.

Axis 2 is interpreted as a complex environmental gradient associated with disturbance through cryoturbation. Low soil moisture and vegetation height, shallow depth of snow and the organic horizon are characteristic of frost-heave features and decrease along axis 2, whereas thaw depth increases along this axis. In general, tundra plots are grouped towards the upper part of the ordination space, and frost-heave features occupy the lower part. The dry tundra plots at Howe Island represent an exception.

The results obtained by the classification are reflected in the ordination analysis (Fig. 2.18). The Cladino-Vaccinietum vitis-idaeae, the Sphagno-Eriophoretum vaginati and the *Anthelia juratzkana-Juncus biglumis* community are clustered in the left portion of the ordination space, which is correlated with low soil pH, warm air temperatures and high shrub cover. The plant communities of the Dryadion integrifoliae (*Dryas integrifolia-Salix arctica* community, Junco biglumis-Dryadetum integrifoliae and Dryado integrifoliae-Caricetum bigelowii) occupy the center of the ordination diagram. They are arranged along a soil moisture and disturbance gradient, with soil moisture increasing and cryogenic activity decreasing from the *Dryas integrifolia-Salix arctica* community toward the Dryado

integrifoliae-Caricetum bigelowii. The plant communities of the Scheuchzerio-Caricetea nigrae (Salici rotundifoliae-Caricetum aquatilis and *Scorpidium scorpioides-Carex aquatilis* community) are located in the upper part of the ordination space, corresponding to high soil moisture conditions, thick organic horizons and shallow thaw depth. The *Braya purpurascens-Puccinellia angustata* community occupies the lower right corner of the diagram, which corresponds to low soil moisture conditions, cool air temperature and great thaw depth.

The DCA axes are scaled in units of the average standard deviation of species turnover (SD, Fig. 2.18). Along a gradient, a complete turnover in species composition of plots occurs in about 4 SD (Hill and Gauch, 1980). Along the complex bioclimate/pH gradient, an almost entire species turnover occurs from the acidic plant communities to the communities of the Dryadion integrifoliae, and another full turnover in species composition occurs between the Dryadion integrifoliae and the *Braya purpurascens-Puccinellia angustata* community. Along the complex disturbance gradient, an almost complete species turnover occurs between the *Scorpidium scorpioides-Carex aquatilis* community and most of the remaining communities.

Plant functional types and floristic analysis

The analyses of plant functional types and floristic affinities show pronounced differences between frost-heave communities and adjacent tundra plots as well as changes along the bioclimate gradient. Total species richness peaks in plant communities in subzone D and is lower in subzone C and E (Fig. 2.19) possibly because subzone D is

warmer than subzone C and has more mineral-rich soils than subzone E. The floristic richness is greatest in the Junco biglumis-Dryadetum integrifoliae with 164 species. The Dryado integrifoliae-Caricetum bigelowii has also a great floristic richness with 155 species, which is consistent with the exceptionally high diversity noted by Matveyeva (1994) in the corresponding Carici arctisibiricae-Hylocomietum alaskani of the Taymir Peninsula, Russia. The wet sedge *Scorpidium scorpioides-Carex aquatilis* community has the poorest floristic diversity with 26 species. Species numbers in all communities are driven by nonvascular species, which usually make up more than 60% of the total species. When comparing frost-heave communities to the surrounding tundra counterparts, frost-heave features usually have relatively greater lichen and liverwort diversity. In contrast, stable tundra communities show greater diversity in forbs and mosses. The species richness of liverworts increases along the bioclimate gradient from north to south, whereas the species richness of forbs, graminoids and mosses peaks in subzone D.

Total plant cover is usually greater in tundra plots than in frost-heave communities (Fig. 2.19). In general, the tundra communities have greater dwarf shrub, graminoid and moss cover, while frost-heave communities support a greater lichen and liverwort cover. The cover of graminoids plays an important role especially in the wet Salici rotundifoliae-Caricetum aquatilis (67%) and *Scorpidium scorpioides-Carex aquatilis* community (73%). The cover of forbs is low in all community types (0-6%), but is highest in the *Dryas integrifolia-Salix arctica* community. Along the bioclimate gradient, total plant cover of frost-heave features increases from north to south

from 49 to 140%, and total plant cover of the surrounding tundra remains relatively constant (79 to 131%). The cover of lichens decreases along the bioclimate gradient, whereas the importance of mosses and liverworts increases from north to south.

Frost-heave features and adjacent tundra communities also show pronounced differences when considering the cover and growth form of lichens (Fig. 2.20). Nonsorted circles exhibit lichen cover values ranging from 21% to 43%, whereas the surrounding tundra plots reach a maximum of only 5%. Nonsorted circles support all three growth forms of lichens, with crustose lichens reaching their maximum cover in the northern sites and fruticose lichen covers increasing towards the south. Foliose lichens are rare on northern nonsorted circles and are only a minor component in the south. In contrast, stable tundra communities do not support the growth of crustose lichens but have small amounts of both fruticose and foliose lichens.

An analysis of the floristic affinities of the vascular plants within each plant community is presented in Fig. 2.21. The analysis considers the flora in three ways modified from the criteria by Walker (1985): major regional units, northern limits of species distribution and geographic range. When comparing plant communities of nonsorted circles and adjacent tundra areas within a subzone, differences are slight. All communities are dominated by arctic-alpine species, which proportion ranges from 39-70%. In general, nonsorted circles seem to support a slightly larger proportion of species with distribution limits farther in the north. Nonsorted circles in subzones C and D support also relatively more North American species, whereas the surrounding tundra communities show a greater proportion of circumpolar species.

Along the bioclimate gradient, the proportion of coastal and arctic-alpine species decreases towards the south from 18 to 0% and from 70 to 39%, respectively, whereas the importance of arctic-boreal species increases from 0 to 31% (Fig. 2.21). The plant communities at the northern end of the bioclimate gradient have a great proportion of species with northern distribution limits in Zone 1 or 2 (up to 36% and 48%, respectively), whereas more than half of the species in southern communities have their distribution limits in Zone 3. However, species with rather warm distribution limits in Zone 4 do not occur in the southern plant communities in subzone E. Most Zone 4 species are *Carex* species limited to the moist nonacidic graminoid tundra in subzone D in this study. All communities are dominated by species with circumpolar ranges, with the importance of circumpolar species increasing towards the south. In contrast, species with their geographic range limited to Northern America occur mostly in the northern sites.

Soil properties

Physical soil properties vary among the different plant communities. Frost-heave communities have greater amounts of bare soil and very thin organic horizons, resulting in lower moisture values of the mineral soil due to evaporation when compared to adjacent tundra communities (Fig. 2.22). The amount of bare ground decreases along the climate gradient from north to south. The depth of the organic horizons and soil moisture are greatest in the stable tundra in subzone D and lowest for the bare nonsorted circles in subzone C. Bulk density of the mineral soil is generally slightly greater for the frost-

heave communities than the surrounding tundra, which might be explained by the different soil textures. When comparing frost-heave features and adjacent tundra within a subzone, the frost-heave features have greater clay contents and less coarse-textured materials (Fig. 2.22), indicating that sorting caused by frost heave is moving coarser materials to the edges of the frost-heave features. Soil texture also varies along the climate gradient, with clay content increasing from north to south. This is caused by the older, more weathered glacial surfaces at the southern end of the gradient when compared to the relatively young alluvial and eolian parent materials on the coastal plain.

The chemical characteristics of the mineral soils associated with the different plant communities depend strongly on soil reaction. Soil pH averages 8.1 in the nonacidic nonsorted circles and 7.7 in the nonacidic stable tundra and drops to 5.2 in the acidic tundra (Fig. 2.23). Frost-heave features have often slightly higher pH values than the adjacent tundra, which can be explained by the lack of thick organic horizons and thus less input of leached organic acids. Total C is greater in the nonacidic tundra than in acidic tundra communities (Fig. 2.23). Inorganic C in the form of carbonates, e.g. $CaCO_3$, is most likely responsible for the greater total C values at nonacidic sites (Ping, pers. comm.), which is supported by the high Ca^{2+} contents at these sites. The calcium-rich carbonates are blown into the sites from the Sagavanirktok River in the form of loess. Total C is slightly lower in the nonacidic frost-heave features (5.0%) than in the surrounding tundra (5.8%). Total N shows a similar pattern, with 0.17% and 0.19% in nonacidic and acidic frost-heave features, respectively, and 0.26% and 0.21% in the

adjacent tundra sites (Fig. 2.23). These results can be explained by less plant biomass in the frost-heave communities and therefore less decomposable material in the soils.

Loess input and pH levels also affect the availability of soil nutrients. The nonacidic nonsorted circles and stable tundra sites have relatively high contents of available Ca^{2+} (means 62 and 46 me/100g, respectively), Mg^{2+} (means 1.85 and 1.65 me/100g) and K^{+} (means 0.13 and 0.17 me/100g, Fig. 2.23). In contrast, the acidic frost-heave features and stable tundra are low in available Ca^{2+} (means 6 and 9 me/100g, respectively), Mg^{2+} (means 0.84 and 1.59 me/100g) and K^{+} (means 0.10 and 0.07 me/100g). Available Na^{+} in the mineral soil decreases along the climate gradient from 2.23 me/100g in the north to 0.01 me/100g in the south (Fig. 2.24). The decrease in Na^{+} is correlated with increasing distance from the ocean and thus decreased salt inputs from the ocean spray. The nonsorted circles and small contraction-crack polygons in subzone C have especially high Na^{+} values. Proximity to the ocean and high evaporation from these barren features result in high salt concentrations in the surface horizon when compared to surrounding tundra areas. High Ca^{2+} concentrations were measured for soils of the Junco biglumis-Dryadetum integrifoliae, where thick $CaCO_3$ deposits cover the soil surface as marl.

Linkages between climate, frost heave and vegetation

The morphology of frost-heave features is strongly controlled by climate (Chernov and Matveyeva, 1997; Walker *et al.*, 2004). We found that at the northern sites in subzone C, the physical constraints of the harsh environment result in low plant cover

and thin organic horizons on both frost-heave features and surrounding tundra. Further south in subzone D, physical processes dominate on frost-heave features and result in sparse vegetation. In contrast, biological processes dominate in the surrounding tundra due to the moderate climate, allowing for denser vegetation and thicker organic layers. Under the warmer climate of the southern-most sites in subzone E, biological processes dominate the landscape morphology and result in poorly developed frost-heave features. Both frost-heave features and the surrounding tundra are completely covered with vegetation and have thick organic horizons.

Climate change in arctic ecosystems is expected to have major effects on vegetation patterns, recession of permafrost and nutrient cycling (Chapin *et al.*, 2004; Hinzman *et al.*, 2005). An alteration of temperature and moisture regimes caused by global climate change will likely result in shifts of vegetation zones and species composition (Chapin *et al.*, 1995). Cryogenic features are most strongly expressed in subzone C and become more vegetated towards the south. They should be highly susceptible to environmental change (Walker *et al.*, 2004). A potential decline in cryoturbation activity due to increased biomass and permafrost degradation due to thawing (Chapin *et al.*, 2004) could lead to local disappearance of frost-heave features in the arctic tundra and a decrease in landscape heterogeneity and biodiversity.

CONCLUSION

We found that well developed frost-heave features display tight linkages among soil, vegetation and cryoturbation activity. Frost-heave features show strong soil-surface

disturbance due to needle-ice formation and frost cracking, having a negative impact on plant roots and resulting in little vegetation cover and shallow organic horizons. In turn, the sparse plant canopy provides only minimal insulation at the soil surface, which results in great thaw depths in late summer, reinforcing frost-heave activity.

We identified and described nine plant associations and communities in the cryoturbated arctic tundra: *Braya purpurascens-Puccinellia angustata* community (dry nonsorted circles, subzone C); *Dryas integrifolia-Salix arctica* community (dry tundra, subzone C); Salici rotundifoliae-Caricetum aquatilis ass. nov. (moist coastal tundra, subzone C); Junco biglumis-Dryadetum integrifoliae ass. nov. (moist nonsorted circles, subzone D); Dryado integrifoliae-Caricetum bigelowii Walker *et al.* 1994 (moist tundra, subzone D); *Scorpidium scorpioides-Carex aquatilis* community (wet tundra, subzone D); Cladino-Vaccinietum vitis-idaeae ass. nov. (dry nonsorted circles and earth hummocks, subzone E); Sphagno-Eriophoretum vaginati Walker *et al.* 1994 (moist tundra, subzone E); and *Anthelia juratzkana-Juncus biglumis* community (wet nonsorted circles, subzone E).

The most important environmental factors resulting in the characteristic species composition of the community types described above are disturbance through cryoturbation, climate, soil pH and soil moisture. The DCA ordination displayed the vegetation types with respect to complex environmental gradients. The first axis of the DCA ordination corresponds to a complex bioclimate/pH gradient, where the percentage of bare soil and pH increase, while air temperature, elevation and shrub cover decrease. The second axis corresponds to a complex disturbance/soil moisture gradient.

Frost-heave features support a greater lichen and liverwort cover, whereas the adjacent tundra areas have a greater cover of dwarf shrubs, graminoids and mosses. The cover of lichens decreases along the bioclimate gradient, whereas the importance of mosses and liverworts increases from north to south. All communities are dominated by arctic-alpine species and taxa with circumpolar geographic ranges.

Frost-heave features have greater amounts of bare ground, thinner organic horizons and lower soil moisture when compared to the surrounding tundra. Soils in the nonacidic tundra are richer in plant-available nutrients than acidic soils, with coastal sites showing high Na^+ concentrations and having smooth soil surfaces due to soil dispersing. Ca^{2+} accumulates in nonsorted circles further inland and results in "cottage cheese" crusts due to aggregation and needle-ice formation.

In correspondence with other studies (Chernov and Matveyeva, 1997; Walker *et al.*, 2004), we found that the morphology of frost-heave features changes along the climatic gradient. Large, almost barren nonsorted circles with a high degree of contraction cracking dominate the landscape in the dry nonacidic tundra in subzone C. In subzone D, nonsorted circles show more vegetation cover and are smaller in diameter. Farther south, the less active nonsorted circles and earth hummocks have thick vegetation mats and resemble the adjacent tundra areas in species composition. Active nonsorted circles are small and sparsely distributed in subzone E.

Thawing of permafrost and a possible shift in plant community composition and vegetation zones might lead to a decline in frost-heave features. The potential loss of frost-heave features and the associated plant communities would especially impact areas

with great floristic differences between frost-heave features and adjacent tundra and result in the loss of landscape heterogeneity.

REFERENCES

Bliss LC, and Matveyeva NV. 1992. Circumpolar arctic vegetation. In *Arctic ecosystems in a changing climate: an ecophysiological perspective*, Chapin FS, III, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J, and Chu EW (eds). Academic Press: San Diego; 59-89.

Bliss LC, Svoboda J, and Bliss DI. 1984. Polar deserts, their plant cover and plant production in the Canadian High Arctic. *Holarctic Ecology* **7**: 305-324.

Bockheim JG, Tarnocai C, Kimble JM, and Smith CAS. 1997. The concept of gelic materials in the new Gelisol order for permafrost-affected soils. *Soil Science* **162**: 927-939.

CAVM Team. 2003. Circumpolar Arctic Vegetation Map. Scale 1:7,500,000. Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service: Anchorage.

Chapin FS, III, Peterson G, Berkes F, Callaghan TV, Angelstam P, Apps M, Beier C, Bergeron Y, Crépin A-S, Danell K, Elmqvist T, Folke C, Forbes B, Fresco N, Juday G, Niemelä J, Shvidenko A, and Whiteman G. 2004. Resilience and vulnerability of northern regions to social and environmental change. *Ambio* **33**: 344-349.

Chapin FS, III, Shaver GR, Giblin AE, Nadelhoffer KG, and Laundre JA. 1995. Response of arctic tundra to experimental and observed changes in climate. *Ecology* **76**: 694-711.

Chernov YI, and Matveyeva NV. 1997. Arctic ecosystems in Russia. In *Ecosystems of the world, vol. 3: Polar and alpine tundra*, Wielgolaski FE (ed). Elsevier: Amsterdam; 361-507.

Cooper DJ. 1986. Arctic-alpine tundra vegetation of the Arrigetch Creek Valley, Brooks Range, Alaska. *Phytocoenologia* **14**: 467-555.

Dierschke H. 1994. *Pflanzensoziologie*. Ulmer Verlag: Stuttgart.

Dierßen K. 1996. *Vegetation Nordeuropas*. Ulmer Verlag: Stuttgart.

Elias SA, Short SK, Walker DA, and Auerbach NA. 1996. Final report: historical biodiversity at remote Air Force sites in Alaska. Legacy Resource Management Program Project, 0742, Department of Defense, Air Force.

Esslinger TL. 1997. A cumulative checklist for the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada. North Dakota State University: Fargo.

Gartner BL, Chapin FS, III, and Shaver GR. 1986. Reproduction of *Eriophorum vaginatum* by seed in Alaskan tussock tundra. *Journal of Ecology* **74**: 1-18.

Gee GW, and Bauder JW. 1986. Particle-size analysis. In *Methods of soil analysis, part 1: Physical and mineralogical methods*, Klute A (ed). Soil Science Society of America, Inc.: Madison; 404-408.

Gelting P. 1955. A West Greenland *Dryas integrifolia* community rich in lichens. *Sv. Bot. Tidskr.* **49**: 295-313.

Hallet B. 1990. Self-organization in freezing soils: from microscopic ice lenses to patterned ground. *Canadian Journal of Physics* **68**: 842-852.

Hallet B, and Prestrud S. 1986. Dynamics of periglacial sorted circles in western Spitzbergen. *Quaternary Research* **26**: 81-99.

Hamilton TD. 1987. Surfacial geologic map of the Philip Smith Mountains Quadrangle, Alaska. Scale 1:125,000. Misc. Field Stud. Map MF-879A. U.S. Geological Survey: Anchorage.

Hartmann H. 1980. Beitrag zur Kenntnis der Pflanzengesellschaften Spitzbergens. *Phytocoenologia* **8**: 65-147.

Haugen RK. 1982. Climate of remote areas in north-central Alaska: 1975-1979 summary. U.S. Army Cold Regions Research and Engineering Laboratory: Hanover, New Hampshire.

Hill MO, and Gauch HG. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* **42**: 47-58.

Hinzman LD, Bettez ND, Bolton WR, Chapin FS, III, Dyurgerov MB, Fastie CL, Griffith B, Hollister RD, Hope A, Huntington HP, Jensen AM, Jia GJ, Jorgenson T, Kane DL, Klein DR, Kofinas G, Lynch AH, Lloyd AH, McGuire AD, Nelson FE, Oechel WC, Osterkamp TE, Racine CH, Romanovsky VE, Stone RS, Stow DA, Sturm M, Tweedie CE, Vourlitis GL, Walker MD, Walker DA, Webber PJ, Welker JM, Winker KS, and Yoshikawa K. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change* **72**: 251-298.

Ignatov MS, and Afonina OM. 1992. Check-list of mosses of the former USSR. *Arctoa* **1**: 1-86.

Jackson ML. 1958. *Soil chemical analysis*. Prentice Hall: Englewood Cliffs.

Johnson AW, and Neiland BJ. 1983. An analysis of plant succession on frost scars 1961-1980. Proceedings on Permafrost: Fourth International Conference. National Academy Press: University of Alaska Fairbanks, Fairbanks.

Kent M, and Coker P. 1992. *Vegetation description and analysis, a practical approach.* John Wiley and Sons: New York.

Kessler MA, Murray AB, and Werner BT. 2001. A model for sorted circles as self-organized patterns. *Journal of Geophysical Research* **106**: 13287-13306.

Kessler MA, and Werner BT. 2003. Self-organization of sorted patterned ground. *Science* **299**: 380-383.

Konstantinova NA, Potemkin AD, and Schljakov RN. 1992. Check-list of the Hepaticae and Anthocerotae of the former USSR. *Arctoa* **1**: 87-127.

Lünterbusch CH, and Daniëls FJA. 2004. Phytosociological aspects of *Dryas integrifolia* vegetation on moist-wet soil in Northwest Greenland. *Phytocoenologia* **34**: 241-270.

Matveyeva NV. 1994. Floristic classification and ecology of tundra vegetation of the Taymyr Peninsula, northern Siberia. *Journal of Vegetation Science* **5**: 813-838.

McCune B, and Mefford MJ. 1999.Multivariate analysis of ecological data, Version 4.10.MjM Software Design, Gleneden Beach.

Mehlich A. 1984. Mehlich No. 3 extractant: a modification of Mehlich No. 2 extractant. *Commun. Soil Sci. and Plant Analysis* **15**: 1409-1416.

Michaelson GJ, Ping CL, and Walker DA. 2005. Biogeochemistry of soils associated with cryptogamic crusts on frost boils in arctic Alaska. *Arctic, Antarctic and Alpine Research*: (in review).

Mueller-Dombois D, and Ellenberg H. 1974. *Aims and methods of vegetation ecology.* John Wiley and Sons: New York.

Peet RK, Knox RG, Case JS, and Allen RB. 1988. Putting things in order; the advantages of detrended correspondence analysis. *American Naturalist* **129**: 434-448.

Peterson RA, and Krantz WB. 2003. A mechanism for differential frost heave and its implications for patterned ground formation. *Journal of Geology* **49**: 69-80.

Peterson RA, Walker DA, Romanovsky VE, Knudson JA, Raynolds MK, and Krantz WB. 2003. A differential frost heave model: cryoturbation-vegetation interactions. In *Proceedings of the Eighth International Conference on Permafrost*, Zürich, Switzerland; 885-890.

Péwé TL. 1975. Quaternary geology of Alaska. Geol. Surv. Prof. pap. 835, U.S. Government Printing Office: Washington D.C.

Ping CL, Bockheim JG, Kimble JM, Michaelson GJ, and Walker DA. 1998. Characteristics of cryogenic soils along a latitudinal transect in Arctic Alaska. *Journal of Geophysical Research* **103**: 28917-28928.

Ping CL, and Moore JP. 1993. Soil classification and climatic zones of Alaska. In *Proceedings of the Sixth International Conference on Permafrost*, Beijing, China; 517-522.

Polunin N. 1951. The real Arctic: suggestions for its delimination, subdivision and characterization. *Journal of Ecology* **39**: 308-315.

Robertson GP, Coleman DC, Bledsoe CS, and Sollins P. 1999. Soil carbon and nitrogen. In *Standard soil methods for long-term ecological research*, Robertson GP, Coleman DC, Bledsoe CS, and Sollins P (eds). Oxford University Press: New York; 89-105.

Rønning O. 1964. *Svalbards flora*. Norsk Polarinst.: Oslo.

Sigafoos RS. 1951. Soil instability in tundra vegetation. *Ohio Journal of Science* **6**: 281-298.

Soil Survey Staff. 1999. *Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys*. U.S. Government Printing Office: Washington D.C.

Thannheiser D. 1991. Die Küstenvegetation der arktischen und borealen Zone. *Berichte der Reinhold-Tüxen-Gesellschaft* **3**: 21-42.

USDA NRCS. 2004. The PLANTS database, version 3.5. National Plant Data Center: Baton Rouge.

Walker DA. 1985. Vegetation and environmental gradients of the Prudhoe Bay region, Alaska. CRREL Report 85-14

Walker DA. 2000. Hierarchical subdivision of arctic tundra based on vegetation response to climate, parent material and topography. *Global Change Biology* **6**: 19-34.

Walker DA, Epstein HE, Gould WA, Kelley AM, Kade A, Knudson JA, Krantz WB, Michaelson GJ, Peterson RA, Ping CL, Raynolds MK, Romanovsky VE, and

Shur Y. 2004. Frost-boil ecosystems: complex interactions between landforms, soils, vegetation and climate. *Permafrost and Periglacial Processes* **15**: 171-188.

Walker DA, and Everett KR. 1991. Loess ecosystems of northern Alaska: regional gradient and toposequence at Prudhoe Bay. *Ecological Monographs* **61**: 437-464.

Walker MD, Walker DA, and Auerbach NA. 1994. Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska. *Journal of Vegetation Science* **5**: 843-866.

Walker MD, Walker DA, Everett KR, and Short SK. 1991. Steppe vegetation on south-facing slopes of pingos, central Arctic Coastal Plain, Alaska, U.S.A. *Arctic and Alpine Research* **23**: 170-188.

Washburn AL. 1956. Classification of patterned ground and review of suggested origins. *Bulletin of the Geological Society of America* **67**: 823-866.

Washburn AL. 1980. *Geocryology: A survey of periglacial processes and environments*. John Wiley and Sons: New York.

Webber PJ. 1978. Spatial and temporal variation of the vegetation and its production, Barrow, Alaska. In *Vegetation and production ecology of an Alaskan Arctic Tundra*, Tieszen LL (ed). Springer Verlag: New York; 37-112.

Weber HE, Moravec J, and Theurillat JP. 2000. International code of phytosociological nomenclature; 3rd edition. *Journal of Vegetation Science* **11**: 739-768.

Westhoff V, and van der Maarel E. 1978. The Braun-Blanquet approach. In *Classification of plant communities*, Whittaker RH (ed). Junk: Den Haag; 287-399.

Young SB. 1971. The vascular flora of St. Lawrence Island with special reference to floristic zonation in the arctic regions. *Contributions of the Gray Herbarium* **102**: 11-115.

Yurtsev BA. 1994. Arctic tundras of Wrangel Island. In *Proceedings of Komarov Botanical Institute.*

Table 2.1. Environmental variables and soil physical and chemical properties for the plant associations and communities of the cryoturbated tundra. Means with standard errors in parentheses.

	Braya purpurascens-Puccinellia angustata comm.	Dryas integrifolia-Salix arctica comm.	Salici rotundifoliae-Caricetum aquatilis ass.	Junco biglumis-Dryadetum integrifoliae ass.	Dryado integrifoliae-Caricetum bigelowii ass.	Scorpidium scorpioides-Carex aquatilis comm.	Cladino-Vaccinietum vitis-idaeae ass.	Sphagno-Eriophoretum vaginati ass.	Anthelia juratzkana-Juncus biglumis comm.
Thaw depth (cm)	79.4 (1.1)	65.0 (1.4)	28.0 (0.3)	88.1 (1.4)	64.9 (1.9)	70.0 (1.8)	60.3 (0.9)	33.6 (1.6)	59.8 (1.9)
Snow depth (cm)	8.1 (2.0)	13.3 (2.7)	19.2 (2.6)	27.0 (1.9)	39.8 (2.5)	58.6 (7.4)	39.7 (4.6)	60.1 (4.4)	63.2 (0.9)
O-horizon depth (cm)	0.0 (0.0)	0.4 (0.2)	26.8 (1.2)	0.2 (0.1)	15.3 (1.5)	25.4 (0.9)	6.4 (1.6)	11.9 (1.0)	0.0 (0.0)
Bare soil (%)	55.0 (11.8)	0.0 (0.3)	0.1 (0.1)	26.3 (4.8)	0.3 (0.2)	2.4 (1.1)	0.0 (0.0)	0.0 (0.0)	10.6 (4.2)
Soil moisture (vol.-%)	28.3 (2.9)	37.3 (2.6)	47.1 (0.4)	39.2 (0.9)	45.2 (2.5)	49.0 (1.9)	35.8 (1.6)	44.1 (1.3)	41.8 (3.3)
Bulk density (g/cm^3)	1.11 (0.04)	0.79 (0.03)	0.82 (0.02)	1.35 (0.04)	1.23 (0.07)	1.34 (0.04)	0.95 (0.05)	1.07 (0.04)	1.13 (0.04)
Sand content (%)	52.1 (3.3)	65.3 (2.3)	36.8 (1.6)	44.9 (2.7)	45.3 (3.3)	43.3 (2.7)	29.8 (1.4)	33.4 (1.9)	28.6 (1.9)
Silt content (%)	31.8 (2.3)	30.1 (2.6)	45.7 (2.0)	34.9 (2.6)	40.8 (3.0)	46.6 (5.8)	44.4 (1.1)	44.9 (1.1)	43.6 (1.5)
Clay content (%)	16.1 (3.9)	4.6 (0.8)	17.5 (2.2)	20.2 (0.6)	13.9 (1.2)	10.1 (3.2)	25.8 (0.8)	21.7 (1.8)	27.8 (1.8)
Soil pH	8.3 (0.1)	7.9 (0.1)	6.5 (0.1)	8.1 (0.1)	7.9 (0.1)	7.7 (0.1)	5.0 (0.1)	5.3 (0.1)	5.2 (0.1)
Total C (%)	4.77 (0.31)	6.30 (0.24)	5.34 (0.11)	5.1 (0.21)	5.78 (0.26)	5.42 (0.83)	3.73 (0.39)	3.46 (0.28)	2.68 (0.55)
Total N (%)	0.11 (0.01)	0.18 (0.03)	0.19 (0.02)	0.18 (0.01)	0.29 (0.03)	0.26 (0.05)	0.21 (0.02)	0.21 (0.02)	0.15 (0.04)
Available Ca^{2+} (me/100g)	39.8 (1.4)	48.3 (1.8)	22.0 (0.8)	67.3 (6.7)	53.2 (2.7)	40.6 (8.3)	5.4 (0.9)	9.2 (0.5)	6.0 (0.9)
Available Mg^{2+} (me/100g)	2.35 (0.12)	1.78 (0.15)	1.14 (0.08)	1.7 (0.18)	1.86 (0.21)	1.20 (0.12)	0.76 (0.10)	1.59 (0.07)	1.07 (0.11)
Available K^+ (me/100g)	0.18 (0.01)	0.14 (0.02)	0.11 (0.01)	0.12 (0.01)	0.18 (0.02)	0.18 (0.02)	0.10 (0.01)	0.07 (0.01)	0.08 (0.01)
Available Na^+ (me/100g)	3.18 (0.61)	0.32 (0.14)	1.42 (0.10)	0.05 (0.01)	0.06 (0.01)	0.06 (0.01)	0.02 (0.01)	0.02 (0.01)	0.02 (0.01)

Table 2.2. Summer warmth indices (SWI) for the study sites (after Walker *et al.* 2004).

Study site	Subzone	SWI (°C mo)
Howe Island	C	9.3
West Dock	C	14.0
Deadhorse	D	19.0
Franklin Bluffs	D	27.0
Sagwon MNT	D	28.2
Sagwon MAT	E	28.2
Happy Valley	E	30.2

Table 2.3. Class, order, alliance and association or community names and habitats of the cryoturbated tundra in the Alaskan Low Arctic.

Undescribed unit Braya purpurascens-Puccinellia angustata comm. Nonsorted circles and small polygons; dry nonacidic tundra; subzone C
C. Carici rupestris-Kobresietea bellardii Ohba 1974 O. Kobresio-Dryadetalia (Br.-Bl.1948) Ohba 1974 A. Dryadion integrifoliae Ohba ex Daniëls 1982 Dryas integrifolia-Salix arctica comm. Stable, dry nonacidic tundra; subzone C Junco biglumis-Dryadetum integrifoliae ass. nov. Nonsorted circles; moist nonacidic tundra; subzone D Dryado integrifoliae-Caricetum bigelowii Walker et al. 1994 Stable, moist nonacidic tundra; subzone D
C. Scheuchzerio-Caricetea nigrae (Nordh. 1936) Tx. 1937 O. Scheuchzerietalia palustris Nordh. 1936 A. Caricion lasiocarpae Vanden Berghen ap. Lebrun et al. 1949 Salici rotundifoliae-Caricetum aquatilis ass. nov. Stable, moist nonacidic coastal tundra; subzone C Scorpidium scorpioides-Carex aquatilis comm. Stable, wet nonacidic tundra; subzone D
C. Loiseleurio-Vaccinietea Eggler 1952 O. Rhododendro-Vaccinietalia Br.-Bl. ap. Br.-Bl. & Jenny 1926 A. Loiseleurio-Diapension (Br.-Bl. Et al. 1939) Daniëls 1982 Cladino-Vaccinietum vitis-idaeae ass. nov. Nonsorted circles and earth hummocks; moist acidic tundra; subzone E Sphagno-Eriophoretum vaginati Walker et al. 1994 Stable, moist acidic tundra; subzone E
C. Salicetea herbaceae Br.-Bl. 1947 O. Salicetalia herbaceae Br.-Bl. 1926 A. Saxifrago-Ranunculion nivalis Nordh. 1943 emend. Dierß. 1984 Anthelia juratzkana-Juncus biglumis comm. Nonsorted circles; moist acidic tundra; subzone E

Table 2.4. Community table of the *Braya purpurascens-Puccinellia angustata* community.

	typicum					Mycobilimbia lobulata var.				
Relevé No.	113	114	110	24	21	25	26	115	111	23
Altitude (m.a.s.l.)	4	6	6	12	15	10	13	6	5	7
Number of vascular taxa	3	2	2	3	2	10	9	9	11	3
Number of nonvascular taxa	2	2	1	2	0	17	18	17	16	10
Total number of taxa	5	4	3	5	2	27	27	26	27	13
Ch/D: Community										
Braya glabella ssp. purpurascens	1	+	+	1	+	+	1	1	+	+
Puccinellia angustata	+	+	+	1	+	+	+	1	+	+
Polyblastia sendtneri	+	+	+	.	.	1	2	2	1	2
D: Mycobilimbia lobulata var.										
Mycobilimbia lobulata	+	+	.	.	.	3	3	3	3	4
Lecanora epibryon	.	.	.	.	.	1	1	1	2	+
Salix ovalifolia	.	.	.	.	.	1	1	+	+	+
Fulgensia bracteata	.	.	.	r	.	+	1	+	+	+
Distichium inclinatum	.	.	.	.	.	+	1	1	1	.
Chrysanthemum integrifolium	.	.	.	.	.	+	1	+	+	.
Collema sp.	.	.	.	.	.	+	1	+	+	.
Polyblastia bryophila	.	.	.	.	.	2	2	1	.	+
Hennediella heimii var. arctica	.	.	.	.	.	1	1	1	.	+
Ctenidium procerrimum	.	.	.	.	.	+	1	.	+	.
Thamnolia subuliformis	.	.	.	.	.	+	r	.	+	.
Orthothecium varia	.	.	.	.	.	+	.	+	+	.
Bryum sp.	.	.	.	.	.	.	1	+	+	.
Cerastium beeringianum	.	.	.	.	.	.	1	+	r	.
Tortula ruralis	.	.	.	r	.	.	1	+	.	+
Draba cinerea	.	.	.	.	.	r	1	.	.	.
Potentilla uniflora	.	.	.	.	.	+	.	+	.	.
Encalypta alpina	.	.	.	.	.	.	1	.	1	.
Megaspora verrucosa	.	.	.	.	.	.	1	.	+	.
Pertusaria dactylina	.	.	.	.	.	+	.	.	+	.
Cirriphyllum cirrosum	.	.	.	.	.	+	.	.	.	+
Pedicularis capitata	.	.	.	.	.	r	r	.	.	.
Cephaloziella arctica	.	.	.	.	.	+	.	+	.	.
Lophozia collaris	.	.	.	.	.	+	.	.	+	.
Artemisia campestris ssp. borealis var. borealis	.	.	.	.	.	r	.	.	r	.
Campylium stellatum	.	.	.	.	.	.	1	+	.	.
Draba sp.	.	.	.	.	.	.	.	+	+	.
Bryoerythrophyllum recurvirostre	.	.	.	.	.	.	.	+	+	.
Encalypta sp.	.	.	.	.	.	.	.	+	.	1
Others										
Androsace chamaejasme	+	.	.	.	.	r	.	.	+	.
Cochlearia groenlandica	.	.	.	+	.	+	.	+	.	.

Single occurrences: Amblystegium serpens (rel. 25: +), Rinodina roscida (25: +), Salix arctica (26: +), Aloina brevirostris (26: +), Encalypta rhaptocarpa (26: +), Arctagrostis latifolia (26: r), Ochrolechia frigida (26: r), Juncus biglumis (115: +), Didymodon rigidulus var. icmadophilus (115: +), Ditrichum flexicaule (115: +), Dryas integrifolia (111: +), Polygonum viviparum (111: +), Saxifraga oppositifolia (111: +), Didymodon sp. (111: +), Distichium capillaceum (23: +).

Table 2.5. Community table of the *Dryas integrifolia-Salix arctica* community.

Relevé No.	112	22	28	116	27
Altitude (m.a.s.l.)	6	8	13	6	17
Number of vascular taxa	16	17	16	14	17
Number of nonvascular taxa	13	8	11	17	7
Total number of taxa	29	25	27	31	24
Ch/regional D: Community					
Salix ovalifolia	2	2	2	1	3
Ctenidium procerrimum	3	3	3	1	2
Chrysanthemum integrifolium	1	1	+	1	1
Festuca baffinensis	+	+	+	1	+
Stellaria longipes	+	+	+	+	+
Cerastium beeringianum	+	+	+	+	+
Melandrium apetalum	r	+	r	+	+
Tortula ruralis	+	1	1	+	.
Draba sp.	+	+	+	.	+
Artemisia campestris ssp. borealis var. borealis	r	+	r	.	+
Didymodon asperifolius	+	+	.	+	.
Ch: Class, order and alliance					
Dryas integrifolia	4	4	3	5	4
Saxifraga oppositifolia	1	1	+	1	1
Pedicularis neoalaskanum	+	+	+	+	1
Others					
Salix arctica	2	3	2	1	2
Ditrichum flexicaule	+	2	2	+	1
Polygonum viviparum	+	+	+	+	+
Thamnolia subuliformis	+	+	+	+	+
Minuartia arctica	+	+	+	.	+
Hylocomium splendens	+	.	+	+	1
Braya glabella ssp. purpurascens	r	r	.	.	r
Distichium capillaceum	1	.	1	.	2
Androsace chamaejasme	+	.	.	1	+
Cochlearia groenlandica	.	r	r	.	+
Campylium stellatum	.	.	+	+	+
Encalypta sp.	.	.	+	+	+
Abietinella abietina	+	1	.	.	.
Tomentypnum nitens	+	.	1	.	.
Lophozia collaris	+	.	.	+	.
Rinodina roscida	+	.	.	+	.
Distichium inclinatum	.	1	.	2	.
Hypnum bambergeri	.	+	.	+	.

Single occurrences: Cephaloziella arctica (rel. 112: +), Collema sp. (112: +), Draba cinerea (22: +), Bryum pseudotriquetrum (28: +), Draba alpina (28: +), Amblystegium serpens (28: +), Aneura pinguis (28: +), Lloydia serotina (28: +), Caloplaca cerina (28: +), Carex rupestris (28: r), Didymodon rigidulus var. icmadophilus (116: +), Lecanora epibryon (116: +), Orthothecium varia (116: +).

Table 2.6. Community table of the Salici rotundifoliae-Caricetum aquatilis ass. nov. Nomenclatural type relevé number marked in bold.

Relevé No.	**98**	102	100	99	101
Altitude (m.a.s.l.)	5	5	5	5	5
Number of vascular taxa	24	16	11	8	9
Number of nonvascular taxa	44	29	23	16	16
Total number of taxa	68	45	34	24	25
Ch/regional D: Association					
Salix rotundifolia	1	+	2	3	2
Poa arctica	+	+	+	+	.
Nephroma expallidum	+	.	+	2	r
Cladonia pyxidata	.	+	+	r	r
Myurella tenerrima	+	+	+	.	.
Saxifraga cernua	+	+	.	+	.
Dicranum majus	+	+	.	+	.
Sanionia uncinata	+	+	.	+	.
Ch: Class, order and alliance					
Carex aquatilis	4	4	3	1	2
Eriophorum angustifolium ssp. triste	1	2	1	3	1
Bryum pseudotriquetrum	+	+	+	.	+
Campylium stellatum	+	+	+	.	+
Limprichtia revolvens	+	+	+	.	+
Saxifraga hirculus	+	+	.	.	+
Hierochloe pauciflora	+	.	+	+	.
Companions					
Salix arctica	+	2	1	1	1
Thamnolia subuliformis	1	+	+	+	+
Cetraria islandica	+	+	+	+	+
Dactylina arctica	+	+	+	+	+
Dryas integrifolia	2	2	2	.	1
Tomentypnum nitens	2	.	1	+	+
Hylocomium splendens	+	.	+	+	+
Polygonum viviparum	+	+	+	.	.
Aulacomnium palustre	+	+	.	+	.
Distichium capillaceum	2	.	+	.	+
Salix planifolia ssp. pulchra	1	.	+	.	1
Stellaria sp.	+	.	.	+	+
Polytrichum strictum	.	.	+	+	+
Salix ovalifolia	2	+	.	.	.
Salix reticulata	1	+	.	.	.
Polytrichastrum alpinum	1	+	.	.	.
Bryoerythrophyllum recurvirostre	1	+	.	.	.
Flavocetraria cucullata	+	+	.	.	.
Cladonia pocillum	+	+	.	.	.
Pedicularis sudetica ssp. albolabiata	+	+	.	.	.
Cinclidium arcticum	+	+	.	.	.
Cladonia ecmocyna	+	+	.	.	.
Dupontia fisheri	+	+	.	.	.
Lecidea ramulosa	+	+	.	.	.
Stellaria longipes	+	+	.	.	.
Ochrolechia frigida	+	+	.	.	.
Bryum sp.	+	+	.	.	.
Distichium inclinatum	+	+	.	.	.
Orthothecium chryseum	+	+	.	.	.
Dicranum sp.	+	+	.	.	.
Oncophorus wahlenbergii	1	.	2	.	.
Hypnum bambergeri	+	.	+	.	.
Cinclidium latifolium	+	.	+	.	.
Pedicularis sp.	+	.	+	.	.
Blepharostoma trichophyllum	+	.	+	.	.
Meesia uliginosa	+	.	+	.	.
Aneura pinguis	+	.	+	.	.
Dicranum angustum	+	.	.	+	.
Peltigera aphthosa	+	.	.	.	+
Cladonia gracilis	.	+	+	.	.
Brachythecium sp.	.	+	.	+	.
Cladonia furcata	.	.	.	+	+

Single occurrences: Drepanocladus brevifolius (rel. 98: 1), Ditrichum flexicaule (98: +), Equisetum variegatum (98: +), Senecio atropurpureus (98: +), Aulacomnium turgidum (98: +), Pseudocalliergon turgescens (98: +), Carex misandra (98: +), Caloplaca tiroliensis (98: +), Equisetum scirpoides (98: +), Hypogymnia subobscura (98: +), Alectoria nigricans (98: +), Calypogeia sphagnicola (98: +), Cladonia uncialis (98: +), Salix phlebophylla (98: +), Dicranum elongatum (102: +), Melandrium apetalum (102: +), Minuartia arctica (102: +), Drepanocladus sp. (102: +), Cladonia amaurocraea (102: +), Sphaerophorus globosus (102: +); Carex bigelowii (100: 1), Dicranum spadiceum (100: +), Solorina bispora (100: +), Polytrichum sp. (100: +), Peltigera leucophlebia (99: 1), Cladonia squamosa (99: r), Aulacomnium *acuminatum (101: +), Cirriphyllum cirrosum (101: +), Cochlearia* groenlandica (101: r).

Table 2.7. Community table of the Junco biglumis-Dryadetum integrifoliae ass. nov. Nomenclatural type relevé numbers marked in bold.

	typicum																					pedicularetosum																							
Relevé No.	69	45	63	**106**	71	9	72	6	31	44	10	43	104	70	33	117	36	2	3	1	118	4	7	**32**	97	5	141	8	96	61	64	30	142	60	105	140	58	59	49	50	51	48
Altitude (m.a.s.l.)	275	20	290	20	280	132	280	132	123	20	130	20	20	280	130	125	130	128	128	128	125	128	133	128	128	133	128	133	128	280	280	123	127	280	20	128	281	280	20	20	20	20
Number of vascular taxa	18	16	13	14	11	16	20	19	13	10	22	11	16	17	14	14	13	14	17	14	12	19	24	28	21	26	23	22	18	25	24	21	20	24	19	19	18	19	13	16	12	10
Number of nonvascular taxa	32	19	27	21	19	25	18	23	20	24	18	22	16	18	15	18	18	12	18	17	14	11	25	23	25	25	20	23	24	28	16	17	18	24	18	18	20	12	16	19	20	17
Total number of taxa	50	35	40	35	30	41	38	42	33	34	40	33	32	35	29	32	31	26	35	31	26	30	49	51	46	51	43	45	42	53	40	38	38	48	37	37	38	31	29	35	32	27
Ch/regional D: Association																																													
Cladonia pocillum	+	+	+	+	+	+	.	+	+	+	+	2	.	.	+	+	+	.	+	.	.	.	+	1	+	+	+	+	+	+	+	+	1	+	+	+	+	1	+	+	+	.
Lecanora epibryon	1	+	+	+	+	+	+	1	+	+	+	.	.	.	1	.	+	.	+	.	.	.	1	1	+	+	+	+	+	1	+	1	2	1	+	+	+	+	+	+	+	.
Carex capillaris	+	.	.	+	1	+	+	+	+	.	1	.	+	+	1	+	+	+	1	1	+	+	+	+	+	+	+	1	+	+	.	+	+	+	.	+	+	+	.	.	.	.
Juncus biglumis	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1	+	+	.	.	.	.	.	+	.	.	.	+	.	.	.	+	+	+	.
Solorina bispora	.	+	+	+	+	+	+	+	+	+	.	+	+	+	.	+	+	+	+	.	+	.	+	r	+	+	.	+	.	.	+	r	.	.	+	.	+	+	+	+	.	.
Polyblastia sendtneri	2	3	2	3	1	2	1	2	2	.	2	4	3	2	2	1	3	2	.	1	1	.	2	1	1	1	.	+	.	.	.	+	.	.	+	.	.	.	.	1	+	.
Aneura pinguis	+	+	+	+	+	+	+	+	+	+	+	.	+	+	+	+	+	r	+	.	+	+	+	+	+	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
D: typicum																																										
Bryum wrightii	.	1	+	+	+	+	+	+	+	+	+	.	+	.	.	+	+	+	.	+	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Nostoc commune	+	+	+	1	+	.	+	.	.	+	.	.	.	+	.	+	1	.	1	+	.	+	+	+	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Bryum sp.	+	+	+	+	+	.	.	.	+	+	+	+	.	+	.	+	.	+	.	+	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.
Hymenostylium recurvirostre	+	+	+	+	+	+	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Pohlia beringiensis	+	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mycobilimbia lobulata	+	.	.	.	.	.	+	+	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
d: wet plots																																										
Eriophorum angustifolium ssp. subarcticum	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	1	+	+	+	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Juncus triglumis	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	1	.	+	+	+	1	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
D: pedicularetosum																																										
Tomentypnum nitens	+	+	+	.	+	+	+	.	.	.	.	+	.	.	.	.	.	.	+	.	.	+	1	+	1	+	2	+	1	2	1	+	2	2	1	1	+	+	.	+	+	r
Pedicularis kanei	.	.	.	.	.	r	+	.	+	.	+	.	.	.	r	.	.	.	.	.	.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	.	.	.
Senecio atropurpureus	.	+	+	.	+	.	.	.	.	.	.	+	.	.	.	.	+	+	+	.	.	.	+	+	+	+	+	.	+	1	+	.	+	1	1	.	1	1	+	+	+	+	.
Dactylina arctica	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	+	+	+	.	+	+	+	.	+	+	.	+	.	.	.	+	+	+	+	+
Minuartia arctica	.	.	.	.	.	.	r	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	1	1	+	1	+	+	1	.	+	1	.	.	1	+	.	.	1	+	.	.	.
Arctostaphylos rubra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	+	.	.	.	.	r	+	+	+	+	1	r	1	+	+	.	+	+	.	+	.	.	.	.	.	.	.
Blepharostoma trichophyllum	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+	+	+	.	.	+	+	.	.	.	.	.	.	+	+
Pedicularis capitata	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	+	+	.	+	+	+	.	.	+	+	.	+	+	.	.	.
Carex scirpoidea	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+	1	+	+	+	.	+	.	.	.	.	.	+
Vulpicida tilesii	.	.	.	.	.	.	.	.	+	.	.	.	.	.	r	.	.	.	.	.	.	.	1	+	1	1	+	+	2	.	.	1	.	.	.	+	.	.	.	.	.	.
Papaver macounii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	+	+	.	.	+	+	.	+	.	.	.	.	.
Parrya nudicaulis	.	.	.	.	r	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	+	+	.	+	.	.	.	+	.	.	+	.	+	.	.	.	.
Cassiope tetragona	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	+	+	1	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Rhododendron lapponicum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	+	.	1	.	.	+	1	.	.	.	.	.	.	.	.	.	.
Pertusaria panyrga	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	2	.	2	.	1	.	.	.	+	.	.	.	+	.	.	.	.	.
Dactylina ramulosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.
Rhytidium rugosum	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	1	+	.	.	1	.	.	+	.	.	.	.	.
Lupinus arcticus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	+	.	.	+	1	.	.	.	.
Ch: Class, order and alliance																																										
Dryas integrifolia	+	+	+	1	+	1	+	1	+	+	1	+	1	+	+	+	1	1	.	+	+	+	**4**	**3**	**2**	**4**	**3**	**4**	**2**	**3**	**3**	**2**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**2**	**2**	**3**
Saxifraga oppositifolia	+	+	.	1	+	1	.	1	+	+	1	1	2	+	2	2	2	1	2	1	2	1	+	1	1	1	+	+	1	.	+	+	1	+	1	1	.	.	1	1	+	1
Hypnum bambergeri	1	.	+	+	+	+	1	+	+	+	+	+	.	.	.	+	.	+	+	+	.	+	1	1	+	+	1	1	2	.	2	1	2	1	1	1	2	.	.	+	+	+
Tofieldia pusilla	+	.	+	.	.	+	.	+	+	.	+	.	.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	.	+	+	+	.	.	.	.	.

| Others | | |

aculeata (6: +), Polytrichum sp. (31: +), Aloina brevirostris (44: +), Bryoerythrophyllum recurvirostre (44: +), Leptobryum pyriforme (10: +), Campylium longicuspis (10: +), Androsace chamaejasme (10: +), Braya glabella ssp. purpurascens (10: +), Drepanocladus brevifolius (104: +), Didymodon rigidulus var. icmadophilus (33: +), Cephaloziella arctica (117: +), Tortella tortuosa (36: +), Aulacomnium turgidum (1: +), Dicranum fragilifolium (1: +), Didymodon spadiceus (1: +), Myurella julacea (1: +), Solorina sp. (118: +), Carex atrofusca (4: 1), Vaccinium uliginosum (32: r), Hypogymnia subobscura (97: +), Cyrtomnium hymenophylloides (97: +), Ochrolechia androgyna (5: 1), Orthothecium varia (141: +), Aulacomnium palustre (141: +), Cladonia amaurocraea (8: r), Cladonia gracilis (96: +), Cladonia squamosa (61: +), Peltigera aphthosa (61: +), Pertusaria bryontha (61: +), Lagotis glauca (61: +), Bartramia ithyphylla (64: +), Alectoria nigricans (64: +), Dicranum acutifolium (60: +), Peltigera leucophlebia (60: +), Sanionia uncinata (59: 2), Stereocaulon sp. (50: +), Megaspora verrucosa (51: +).

Table 2.8. Community table of the Dryado integrifoliae-Caricetum bigelowii.

	Lupinus arcticus var.					*Carex scirpoidea* var.										*Eriophorum angustifolium* ssp. subarcticum var.				
Relevé No.	29	67	55	68	65	12	34	13	11	35	46	18	19	47	20	38	41	39	40	42
Altitude (m.a.s.l.)	270	280	280	275	270	133	126	133	130	130	130	130	134	130	130	22	20	21	20	20
Number of vascular taxa	30	42	38	26	18	24	28	23	23	27	35	18	22	25	16	19	18	19	13	12
Number of nonvascular taxa	28	30	27	22	15	18	20	17	14	13	20	14	11	24	12	21	23	21	14	17
Total number of taxa	58	72	65	48	33	42	48	40	37	40	55	32	33	49	28	40	41	40	27	29
Ch/regional D: Association																				
Salix reticulata	1	2	2	2	1	1	1	+	+	+	1	+	1	2	+	2	2	1	1	2
Carex bigelowii	2	+	3	3	2	1	1	2	+	1	+	.	1	1	2	+	+	1	1	.
Arctostaphylos rubra	+	2	2	1	2	2	1	2	2	+	2	+	+	2	1	.	.	.	.	.
Papaver macounii	+	+	+	+	+	+	+	+	+	.	+	.	.	+	.	+	+	+	.	+
Saussurea angustifolia	+	+	+	+	+	1	+	+	+	1	+	+	.	.	.	.	.	.	.	.
***D: Lupinus arcticus* var.**																				
Hylocomium splendens	3	3	4	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aulacomnium turgidum	1	2	2	1	+	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1
Rhytidium rugosum	1	+	2	1	2	+	+	+	.	1	.	.	.	.	.	.	.	.	.	.
Lupinus arcticus	+	1	1	+	+	.	1	r	.	1	.	.	.	.	.	.	.	.	.	.
Dicranum spadiceum	1	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Equisetum arvense	+	1	+	.	1	.	.	+	+	.	.	.	+	.	.	.	.	.	.	.
Saxifraga hieracifolia	+	+	r	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Aulacomnium acuminatum	+	+	.	+	2	.	.	.	.	+	.	.	.	.	.	.	+	.	.	+
Ptilidium ciliare	+	.	1	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Masonhalea richardsonii	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stellaria sp.	.	+	+	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix glauca	1	+	1	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Cladonia pyxidata	+	+	+	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.
Tofieldia pusilla	+	+	+	.	.	.	+	.	.	.	+	.	.	+	.	.	.	.	.	.
Dicranum elongatum	+	+	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pyrola grandiflora	+	r	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygonum bistorta var. plumosum	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene acaulis	+	+	.	+	.	.	.	.	+	+	.	.	.	+	.	.	.	.	.	.
Saxifraga nelsoniana	r	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lagotis glauca	r	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Orthilia secunda	.	+	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Peltigera aphthosa	.	+	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Cladonia gracilis	.	+	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stellaria longipes	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Peltigera sp.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pyrola asarifolia	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Empetrum nigrum ssp. hermaphroditum	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ledum palustre ssp. decumbens	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Peltigera leucophlebia	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anastrophyllum minutum	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Senecio resedifolius	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
D: Carex scirpoidea var.																				
Carex scirpoidea	.	.	.	.	.	+	+	.	+	+	+	+	1	.	+	.	.	.	.	.
Cladonia pocillum	.	.	+	.	.	+	+	1	+	.	1	.	.	+	.	.	.	.	.	.
Bryum pseudotriquetrum	.	.	.	.	.	+	+	+	+	.	.	+	+	.	.	.	.	+	.	.
Kobresia myosuroides	.	.	.	.	.	1	1	.	+	1	.	.	.	.	.	.	.	.	.	.
Draba alpina	.	.	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.
Ctenidium molluscum	.	.	.	.	.	+	.	+	.	.	.	+	.	.	.	.	.	.	.	.
Carex rupestris	.	.	.	.	.	.	+	+	.	+	.	.	.	.	.	.	.	.	.	.
D: Eriophorum angustifolium ssp. subarcticum var.																				
Eriophorum angustifolium ssp. subarcticum	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	3	4	3	2	4
Drepanocladus brevifolius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	2	+	2
Orthothecium chryseum	.	+	.	.	.	.	.	.	.	.	1	+	.	+	.	1	1	+	1	1
Campylium stellatum	.	+	.	.	.	+	.	.	.	.	.	.	.	.	+	+	2	+	+	2
Catoscopium nigritum	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	2	+	+	1	+
Calliergon giganteum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	+	+	+
Cinclidium arcticum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	.
Limprichtia revolvens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	.
Cirriphyllum cirrosum	.	.	.	.	.	+	.	.	.	.	+	+	.	.	.	+	+	+	.	+
Pseudocalliergon turgescens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	+
Pedicularis sudetica ssp. albolabiata	.	+	.	.	.	.	.	.	.	.	+	.	.	+	.	+	.	+	+	.
Drepanocladus sp.	.	+	.	.	.	.	.	.	+	.	.	+	.	.	.	.	+	+	.	+
Saxifraga oppositifolia	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	+	+	.	r
Callialaria curvicaulis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	2	.
Ch: Class, order and alliance																				
Dryas integrifolia	2	2	2	2	2	3	3	2	2	3	2	3	2	3	3	2	2	2	2	2
Hypnum bambergeri	+	.	+	2	.	2	1	2	2	1	+	.	1	+	1	+	+	.	+	+

Pedicularis capitata	+	+	+	+	+	+	+	+	+	+	+	.	+	+	+	.	.	.	.	.
Pedicularis kanei	+	+	+	.	+	.	+	+	+	+	+	+	+	+	.	+	.	.	.	.
Others																				
Tomentypnum nitens	3	3	3	2	2	3	3	3	3	2	2	3	2	3	3	2	2	2	1	3
Eriophorum angustifolium ssp. triste	+	1	2	+	+	1	+	1	1	+	2	2	1	2	2	+	+	.	+	+
Senecio atropurpureus	+	+	+	+	+	+	+	+	+	.	+	+	+	+	+	+	+	+	+	+
Polygonum viviparum	+	+	+	+	.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Thamnolia subuliformis	+	1	1	+	+	1	1	1	1	1	+	+	+	+	+	+	+	+	.	.
Carex membranacea	.	1	+	+	.	+	+	1	1	1	2	1	2	1	2	+	+	1	2	+
Ditrichum flexicaule	.	1	1	+	.	1	1	1	1	2	1	1	1	1	1	1	1	1	+	1
Flavocetraria cucullata	+	1	1	1	+	+	+	1	1	1	1	+	+	+	+	.	.	+	.	.
Cetraria islandica	+	+	+	+	+	+	+	1	+	+	+	+	+	+	+	.	.	+	.	.
Cardamine hyperborea	+	+	+	+	.	+	.	+	+	+	+	+	+	+	+	+	+	+	.	.
Salix arctica	.	.	+	.	.	1	1	1	1	2	2	1	2	2	2	2	1	2	1	1
Equisetum variegatum	.	1	.	.	.	r	+	+	+	+	+	.	+	+	+	+	+	1	+	+
Dactylina arctica	+	+	+	.	.	+	+	+	+	+	+	.	+	+	.	+	+	+	.	.
Distichium capillaceum	.	1	1	.	.	+	+	+	1	+	+	+	.	.	.	1	+	1	+	1
Cassiope tetragona	1	+	1	+	.	1	1	1	1	1	1	1	1	+	.	.	.	.	.	.
Eriophorum vaginatum	1	+	2	1	.	.	.	.	.	.	1	2	3	1	1	+	+	1	+	.
Flavocetraria nivalis	+	+	+	.	.	+	+	+	+	1	+	+	+	+	.	.	.	.	.	.
Salix lanata ssp. richardsonii	.	+	.	.	.	+	.	+	.	.	2	.	+	1	+	1	+	1	1	+
Arctagrostis latifolia	+	+	+	+	.	+	+	.	.	.	.	r	+	.	.	+	+	+	.	.
Parrya nudicaulis	+	+	+	.	.	+	+	+	+	+	+	.	+	.	.	.	.	.	.	.
Minuartia arctica	.	+	+	+	+	+	+	+	+	1	+	.	.	.	.	.	.	.	.	.
Astragalus umbellatus	.	1	+	.	+	1	1	+	1	+	.	.	.	.	.	.	.	.	.	.
Bryum sp.	.	.	.	.	.	.	.	+	.	+	+	.	+	+	.	.	.	+	.	+
Carex vaginata	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	.	.	+	r	.
Vaccinium uliginosum	.	r	+	r	.	.	+	.	.	+	+	.	.	.	.	.	.	.	.	.
Oxytropis maydelliana	.	+	+	.	+	.	+	.	.	1	r	.	.	.	.	.	.	.	.	.
Distichium inclinatum	.	+	+	.	.	.	.	.	.	.	1	.	.	1	.	+	.	.	.	.
Pedicularis langsdorfii	.	.	.	+	.	.	.	.	.	.	+	r	+	+	.	.	.	.	.	.
Solorina bispora	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	+	+	.	.	.
Orthothecium strictum	.	.	+	.	.	.	.	.	.	.	+	.	.	+	.	.	+	.	.	.
Pertusaria panyrga	+	.	r	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Cladonia amaurocraea	+	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Rumex arcticus	.	+	+	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
Papaver sp.	.	r	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.
Carex capillaris	.	.	+	.	.	.	.	.	.	.	.	r	.	.	.	.	+	.	.	.
Carex rariflora	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	r	.	.	r
Encalypta alpina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	+

Additional taxa with two or less occurrences: Cetraria laevigata (rel. 29: +, 19: +), Barbilophozia barbata (29: +, 20: +), Solorina sp. (67: +, 34: +), Oxytropis sp. (67: +, 46: +), Pohlia beringiensis (67: +, 47: +), Didymodon rigidulus var. icmadophilus (67: +, 38: +), Peltigera rufescens (68: +, 12: +), Peltigera scabrosa (68: +, 13: +), Stereocaulon alpinum (34: +, 13: 1), Campylium longicuspis (34: +, 35: +), Rhododendron lapponicum (34: +, 35: +), Ctenidium procerriumum (34: +, 38: +), Chrysanthemum integrifolium (35: r, 46: r), Didymodon rigidulus (46: +, 47: +), Splachnum sp. (46: +, 47: +), Tetraplodon urceolatus (46: +, 47: +), Dicranum fragilifolium (18: +, 20: +), Scorpidium scorpioides (18: +, 38: +), Tortella tortuosa (47: +, 41: +), Carex atrofusca (47: +, 39: +), C. misandra (47: +, 39: +), Meesia uliginosa (47: +, 39: +), Aulacomnium palustre (29: +), Dicranum sp. (29: +), Pleurozium schreberi (29: +), Tritomaria quinquedentata (29: +), Nephroma expallidum (29: r), Ochrolechia androgyna (29: r), Antennaria friesiana (67: +), Bartramia ithyphylla (67: +), Carex aquatilis (67: +), Cyrtomnium hymenophylloides (67: +), Encalypta sp. (67: +), Mycobilimbia lobulata (55: +), Vaccinium vitis-idaea (55: +), Ochrolechia frigida (55: r), O. upsaliensis (55: r), Pertusaria bryontha (55: r), Poa arctica (55: r), Rinodina turfacea (55: r), Blepharostoma trichophyllum (68: +), Cladonia coccifera (68: +), Dicranum acutifolium (68: +), Cladonia fimbriata (65: +), Peltigera malacea (65: +), Thalictrum alpinum (12: +), Abietinella abietina (34: +), Vulpicida tilesii (34: +), Lophozia sp. (13: +), Stereocaulon sp. (11: 1), Hypnum sp. (11: +), Encalypta longicolla (46: +), Caloplaca tiroliensis (47: +), Leptobryum pyriforme (47: +), Tortella fragilis (20: +), Carex rotundata (38: +), Brachythecium sp. (41: +), Carex sp. (41: +), Myurella julacea (41: +), Bryoerythrophyllum recurvirostre (39: +), Pohlia sp. (42: +).

Table 2.9. Community table of the *Scorpidium scorpioides-Carex aquatilis* community.

Relevé No.	15	14	16	17	37
Altitude (m.a.s.l.)	128	128	128	128	130
Number of vascular taxa	10	11	9	11	8
Number of nonvascular taxa	7	7	1	1	9
Total number of taxa	17	18	10	12	17
Ch/regional D: Community					
Pedicularis sudetica ssp. albolabiata	1	+	1	1	+
Carex saxatilis	+	+	+	+	.
Ch: Class, order and alliance					
Eriophorum angustifolium ssp. subarcticum	4	4	4	4	3
Scorpidium scorpioides	1	1	1	1	1
Equisetum variegatum	+	+	+	+	+
Carex aquatilis	+	+	+	.	1
Carex atrofusca	+	+	.	+	.
Campylium stellatum	+	+	.	.	+
Others					
Salix arctica	+	r	+	+	+
Eriophorum vaginatum	+	+	.	r	+
Distichium capillaceum	+	+	.	.	+
Ditrichum flexicaule	+	+	.	.	+
Catoscopium nigritum	+	+	.	.	+
Carex bigelowii	.	.	+	+	+
Limprichtia cossonii	+	+	.	.	.
Carex rariflora	+	.	.	+	.
Pedicularis parviflora	+	.	.	+	.
Salix lanata ssp. richardsonii	.	+	+	.	.

Single occurrences: Calliergon giganteum (rel. 15: +), Pseudocalliergon turgescens (14: +), Dryas integrifolia (14: r), Equisetum arvense (14: r), Equisetum scirpoides (16: +), Carex rotundata (17: +), Aneura pinguis (37: +), Bryum sp. (37: +), Carex sp. (37: +), Meesia uliginosa (37: +), Orthothecium strictum (37: +).

Table 2.10. Community table of the Cladino-Vaccinietum vitis-idaeae ass. nov. Nomenclatural type relevé number marked in bold.

	Racomitrium lanuginosum var.										Carex bigelowii var.				
Relevé No.	73	78	80	90	76	92	74	**91**	88	89	93	94	95	83	82
Altitude (m.a.s.l.)	300	300	300	334	300	332	300	332	328	333	315	315	310	320	320
Number of vascular taxa	12	13	15	11	12	16	10	12	12	11	8	10	12	12	10
Number of nonvascular taxa	30	30	27	26	32	31	27	33	29	23	27	16	19	21	16
Total number of taxa	42	43	42	37	44	47	37	45	41	34	35	26	31	33	26
Ch/regional D: Association															
Anastrophyllum minutum	+	2	1	1	1	1	+	1	1	1	+	+	+	+	+
Cladina arbuscula	+	+	+	1	1	2	1	3	+	.	+	1	1	1	.
Dicranum spadiceum	+	1	2	.	1	1	1	1	+	.	+	+	.	.	.
Polytrichum hyperboreum	+	+	+	.	1	.	+	+	1	+	.	.	.	.	.
D: Racomitrium lanuginosum var.															
Racomitrium lanuginosum	3	2	2	2	3	2	3	2	2	2	.	.	2	.	.
Arctagrostis latifolia	+	2	1	1	2	2	1	+	+	+	.	.	.	.	.
Pertusaria dactylina	+	+	+	.	+	.	+	.	+	1	.	.	.	.	.
Senecio atropurpureus	1	+	+	.	+	+	+	.	.	.	.	.	.	.	+
Eriophorum vaginatum	1	+	1	1	.	.	1	.	.	.	.	1	.	.	.
Salix phlebophylla	+	1	2	.	+	.	1	.	.	.	.	.	.	.	.
Cladonia gracilis ssp. elongata	+	+	1	.	.	.	1	.	.	1	+	.	.	.	.
Rhytidium rugosum	+	1	+	.	1	.	.	.	.	.	.	.	.	.	.
Pertusaria panyrga	+	+	.	+	.	+	.	.	.	.	.	.	.	.	.
Lophozia ventricosa	+	.	.	.	+	.	+	+	.	.	.	.	.	.	.
Cladonia cenotea	.	.	+	+	+	.	.	.	.	+	.	.	.	.	.
Cladonia deformis	.	.	+	+	.	+	.	+	.	.	.	.	.	.	.
Rubus chamaemorus	.	.	.	2	.	+	.	1	.	r	.	.	.	.	.
Calamagrostis sp.	.	.	.	.	.	+	.	1	1	1	.	.	.	.	.
Cladonia pleurota	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.
Nephroma expallidum	+	.	.	.	+	.	.	.	1	.	.	.	.	.	.
Cladonia gracilis	.	.	.	+	.	1	.	.	1	.	.	.	.	.	.
Barbilophozia binsteadii	.	.	.	+	.	+	.	+	.	.	.	.	.	.	.
D: Carex bigelowii var.															
Carex bigelowii	.	+	.	.	.	1	.	.	1	2	2	1	3	2	2
Cetraria islandica	.	+	.	.	+	.	+	.	.	.	+	+	+	+	.
Polytrichum strictum	.	.	.	+	.	+	.	.	.	.	+	+	.	.	+
Cladonia gracilis ssp. vulnerata	.	.	+	.	.	.	.	+	.	.	.	.	1	2	+
Andromeda polifolia	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.
Nephroma arcticum	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.
Ch: Class, order and alliance															
Vaccinium vitis-idaea	2	2	2	3	2	2	2	2	1	2	3	3	2	2	2
Dicranum elongatum	2	2	2	3	1	2	3	3	2	3	1	1	1	1	1
Ledum palustre ssp. decumbens	2	1	2	1	2	2	2	2	1	2	2	3	2	1	2
Betula nana	1	1	1	+	1	2	1	1	1	1	3	2	2	2	2
Flavocetraria cucullata	1	+	+	1	1	1	+	2	1	+	+	+	+	+	1
Empetrum nigrum ssp. hermaphroditum	1	.	1	2	+	2	.	2	1	.	2	+	2	2	2
Cladonia amaurocraea	+	+	.	+	+	+	1	+	+	+	1	.	.	.	+
Others															
Polygonum bistorta var. plumosum	1	2	2	+	1	1	1	1	+	+	1	+	2	2	1
Aulacomnium turgidum	+	1	1	1	2	1	1	1	1	+	1	+	1	1	2
Dactylina arctica	+	+	+	+	+	1	+	+	+	r	+	+	+	+	.
Cladina rangiferina	+	1	+	2	+	2	1	1	3	1	1	.	2	2	3
Hylocomium splendens	+	1	1	+	2	+	2	1	+	.	3	2	3	2	2
Cassiope tetragona	+	1	+	1	1	1	2	.	+	+	+	+	1	1	1
Petasites frigidus	.	2	1	1	2	2	.	1	+	+	.	1	1	+	1
Thamnolia subuliformis	+	+	+	+	+	+	1	+	+	+	.	.	+	.	.
Peltigera leucophlebia	+	1	1	.	+	.	.	.	1	1	1	2	+	.	1
Cladonia fimbriata	+	.	+	.	+	+	+	+	+	+	+	.	.	.	+
Dicranum acutifolium	+	1	.	+	1	.	+	.	1	+	.	.	+	+	.
Cladina stygia	.	+	+	.	.	+	.	+	.	.	2	1	1	.	+
Cladonia uncialis	1	.	.	+	.	.	.	+	1	1	.	.	+	+	.
Cladonia chlorophaea	.	.	+	.	+	+	+	+	.	.	+	+	.	.	.
Pleurozium schreberi	.	.	.	+	.	.	.	+	+	+	+	2	.	.	+
Peltigera malacea	+	+	.	.	.	+	.	+	.	.	+	.	.	.	+
Pedicularis lapponica	+	+	.	.	.	1	.	.	.	r	.		+	+	.
Cetraria laevigata	.	.	.	+	.	+	.	+	.	.	1	.	+	+	.

Dicranum groenlandicum	.	.	.	+	.	2	.	.	+	.	2	.	1	3	.
Ditrichum flexicaule	+	+	.	.	.	.	.	.	+	.	+	.	.	.	+
Peltigera aphthosa	.	.	.	+	.	1	1	1	.	.	.	.	.	+	.
Flavocetraria nivalis	.	.	.	.	+	.	+	.	+	.	+	.	+	.	.
Ptilidium ciliare	.	.	.	.	.	+	.	1	1	+	+	.	.	.	.
Peltigera scabrosa	.	+	.	.	.	.	.	+	.	.	.	1	.	+	.
Pedicularis labradorica	.	.	+	.	.	.	.	+	+	.	.	.	.	+	.
Pedicularis oederi	.	.	.	.	.	+	.	+	.	.	.	.	.	+	+
Cladina mitis	.	.	.	.	.	+	.	.	1	3	.	.	.	+	.
Salix planifolia ssp. pulchra	.	+	.	.	.	.	1	.	.	.	.	1	.	.	.
Lophozia jurensis	.	+	.	.	.	.	.	.	.	.	+	.	.	+	.
Vaccinium uliginosum	.	.	1	.	+	.	.	.	.	.	.	.	+	.	.
Luzula arctica	.	.	.	.	r	.	.	.	r	.	.	.	.	+	.

Additional taxa with two or less occurrences: Hypnum holmenii (rel. 73: +, 80: +), Sphaerophorus globosus (73: +, 74: +), Cladonia coccifera (78: +, 76: +), Luzula confusa (80: +, 92: +), Stellaria sp. (80: r, 92: +), Lophozia savicziae (80: +, 88: +), Dicranum angustum (80: +, 93: +), Pedicularis kanei (90: +, 91: +), Alectoria nigricans (76: +, 92: +), Lophozia excisa (76: +, 92: +), Cladonia pyxidata (76: +, 74: +), Alectoria ochroleuca (76: +, 74: r), Pohlia nutans (76: +, 83: +), Hypogymnia subobscura (74: +, 89: +), Cladonia sulphurina (91: +, 89: +), Arctostaphylos rubra (73: 2), Blepharostoma trichophyllum (73: +), Bryocaulon divergens (78: +), Pohlia sp. (78: +), Cladonia cyanipes (80: +), Ochrolechia androgyna (90: +), Aulacomnium palustre (76: +), Calypogeja muelleriana (92: +), Cladonia cornuta (92: +), Baeomyces rufus (91: +), Cladonia macroceras (91: +), Cladonia squamosa (91: +), Polytrichum sp. (91: +), Authelia juratzkana (88: +), Lophozia sp. (88: +), Ochrolechia inaequatula (89: +), Calamagrostis canadensis (95: +), Cephalozia pleniceps (83: +), Lophozia longiflora (82: +).

Table 2.11. Community table of the Sphagno-Eriophoretum vaginati.

Relevé No.	86	77	75	84	87	81	85	62	79	66
Altitude (m.a.s.l.)	320	300	300	315	315	300	320	300	290	315
Number of vascular taxa	16	13	13	14	12	15	16	16	11	12
Number of nonvascular taxa	23	28	33	23	21	42	26	32	30	20
Total number of taxa	39	41	46	37	33	57	42	48	41	32
Ch/regional D: Association										
Eriophorum vaginatum	3	3	3	3	3	3	3	3	3	3
Sphagnum warnstorfii	2	1	+	2	2	1	2	2	2	2
Salix planifolia ssp. pulchra	1	1	2	2	2	2	1	2	2	1
Sphagnum girgensohnii	+	1	2	1	1	1	1	2	.	.
Pedicularis lapponica	+	+	+	+	+	.	+	.	+	.
Sphagnum angustifolium	2	+	+	2	1	.	1	.	.	2
Saxifraga nelsoniana	+	+	+	.	.	+	.	+	+	.
Ch: Class, order and alliance										
Betula nana	3	2	2	3	3	2	3	2	2	2
Ledum palustre ssp. decumbens	2	2	1	2	2	2	2	2	1	1
Vaccinium vitis-idaea	1	2	1	2	2	2	2	2	1	2
Flavocetraria cucullata	+	+	+	+	+	1	+	1	+	.
Dicranum elongatum	+	+	+	+	+	2	.	.	2	+
Empetrum nigrum ssp. hermaphroditum	2	.	+	2	1	+	2	+	.	1
Cladonia amaurocraea	.	+	.	+	+	+	.	+	+	+
Others										
Hylocomium splendens	2	3	2	2	2	1	3	2	2	1
Cassiope tetragona	1	2	2	1	1	2	1	1	2	1
Aulacomnium turgidum	2	1	1	2	1	1	2	1	2	+
Polygonum bistorta var. plumosum	2	2	1	1	1	1	+	1	+	+
Dactylina arctica	+	+	+	+	+	+	+	1	+	+
Petasites frigidus	+	+	+	+	+	.	1	+	+	+
Senecio atropurpureus	+	+	+	+	.	+	+	+	+	.
Cladina stygia	1	+	+	.	+	+	+	.	+	+
Anastrophyllum minutum	+	+	1	.	.	2	+	+	2	+
Tomentypnum nitens	+	.	r	+	+	+	+	.	+	+
Ptilidium ciliare	+	.	+	1	1	.	+	.	+	+
Cladina rangiferina	1	.	.	+	+	1	+	+	+	.
Peltigera leucophlebia	1	+	+	+	+	1	.	.	.	.
Cladina arbuscula	+	+	+	.	+	+	.	+	.	.
Polytrichum sp.	+	+	+	.	.	+	+	.	+	.
Peltigera scabrosa	+	+	+	.	.	.	+	+	.	+
Pleurozium schreberi	+	.	+	1	1	.	.	.	+	+
Carex bigelowii	1	.	.	1	1	.	1	+	.	+
Blepharostoma trichophyllum	.	1	1	.	.	+	.	+	1	+
Cetraria islandica	+	+	.	+	.	+	.	.	+	.
Thamnolia subuliformis	.	+	+	.	.	+	.	+	+	.
Dicranum acutifolium	.	2	.	+	.	1	+	.	1	.
Dicranum angustum	.	.	2	+	.	+	.	.	+	+
Cetraria laevigata	.	.	.	+	+	r	+	.	.	+
Dicranum groenlandicum	1	.	.	1	1	.	1	.	.	.
Vaccinium uliginosum	1	.	.	1	.	.	.	+	.	+
Nephroma arcticum	+	.	.	.	.	+	+	+	.	.
Barbilophozia binsteadii	.	+	+	.	.	+	.	.	+	.
Arctagrostis latifolia	.	+	+	.	.	+	.	+	.	.
Peltigera malacea	.	+	.	.	+	.	+	+	.	.
Hypnum holmenii	.	.	+	.	.	+	+	.	+	.
Pedicularis labradorica	+	.	.	.	+	.	+	.	.	.
Ditrichum flexicaule	+	.	.	.	.	+	.	.	+	.
Nephroma expallidum	.	+	+	.	.	.	+	.	.	.
Tritomaria quinquedentata	.	+	+	.	.	.	.	.	.	+
Pedicularis oederi	.	+	.	r	.	.	r	.	.	.
Aulacomnium palustre	.	+	.	.	.	+	.	1	.	.
Sphagnum balticum	.	+	.	.	.	.	+	+	.	.
Lophozia ventricosa	.	.	+	.	.	.	.	.	+	+
Cladonia gracilis ssp. vulnerata	.	.	.	+	+	+	.	.	.	.
Cladonia cyanipes	.	.	.	.	.	+	+	.	+	.
Cladonia fimbriata	.	.	.	.	.	+	+	+	.	.
Cladonia deformis	.	.	.	.	.	+	.	+	.	+
Peltigera aphthosa	.	.	.	.	.	.	1	1	+	.

Cephalozia pleniceps	.	+	+	.	.	.	.	.	.	.
Calypogeia sphagnicola	.	+	.	.	.	+	.	.	.	.
Dicranum spadiceum	.	.	+	.	.	+	.	.	.	.
Barbilophozia kunzeana	.	.	+	.	.	.	.	.	+	.
Calypogeia muelleriana	.	.	+	.	.	.	.	.	+	.
Dicranum sp.	.	.	.	+	.	.	.	2	.	.
Salix phlebophylla	.	.	.	.	.	+	.	+	.	.
Flavocetraria nivalis	.	.	.	.	.	+	.	+	.	.
Sphaerophorus globosus	.	.	.	.	.	+	.	+	.	.

Single occurrences: Andromeda polifolia (rel. 86: r), Cephalozia bicuspidata (75: +), Peltigera sp. (75: +), Rhytidium rugosum (84: +), Polytrichum strictum (87: +), Calamagrostis sp. (81: +), Saussurea angustifolia (81: +), Cladonia cenotea (81: +), C. pocillum (81: +), C. uncialis (81: +), Drepanocladus sp. (81: +), Lophozia savicziae (81: +), Pertusaria dactylina (81: +), Rinodina turfacea (81: +), Luzula arctica (81: r), Calamagrostis canadensis (85: +), Stellaria sp. (85: r), Salix arctica (62: +), Alectoria nigricans (62: +), A. ochroleuca (62: +), Bryocaulon divergens (62: +), Cetraria aculeata (62: +), Cladonia coccifera (62: +), C. cornuta (62: +), C. gracilis (62: +), Dactylina ramulosa (62: +), Polytrichastrum alpinum (62: +), Lophozia longiflora (79: +), Pertusaria panyrga (79: +), Pedicularis capitata (66: +), Aneura pinguis (66: +).

Table 2.12. Community table of the *Anthelia juratzkana-Juncus biglumis* community.

Relevé No.	57	54	53	52	56
Altitude (m.a.s.l.)	305	310	305	305	305
Number of vascular taxa	9	6	8	11	7
Number of nonvascular taxa	19	16	24	16	7
Total number of taxa	28	22	32	27	14
Ch/regional D: Community					
Dicranella subulata	1	1	2	+	+
Jungermannia sp.	+	+	2	.	+
Jungermannia confertissima	+	+	+	.	.
Cephalozia bicuspidata	+	+	+	.	.
Juncus biglumis	+	+	.	1	.
Ch: Class, order and alliance					
Anthelia juratzkana	2	2	+	4	3
Luzula arctica	+	.	2	2	.
Others					
Vaccinium vitis-idaea	2	+	1	1	+
Hylocomium splendens	1	1	2	+	+
Eriophorum vaginatum	1	+	+	1	1
Ledum palustre ssp. decumbens	1	r	+	1	+
Betula nana	+	r	+	r	+
Cetraria islandica	1	+	+	r	.
Cassiope tetragona	1	.	1	+	+
Dactylina arctica	+	+	+	.	.
Cladina rangiferina	2	+	.	r	.
Cladonia fimbriata	+	+	.	.	+
Cladonia amaurocraea	+	.	+	+	.
Aulacomnium turgidum	+	.	r	r	.
Empetrum nigrum	+	.	+	.	1
Flavocetraria cucullata	.	+	2	+	.
Vaccinium uliginosum	.	.	+	r	+
Lophozia sudetica var. sudetica	+	+	.	.	.
Lophozia ventricosa	+	+	.	.	.
Anastrophyllum minutum	+	.	+	.	.
Salix planifolia ssp. pulchra	r	.	.	r	.
Cladonia gracilis	.	+	+	.	.
Pohlia cruda	.	+	+	.	.
Peltigera leucophlebia	.	2	.	.	1
Cladonia chlorophaea	.	.	1	+	.
Cladina mitis	.	.	r	+	.
Lophozia sp.	.	.	+	.	+

Single occurrences: Cladonia uncialis (53: +), Dicranum spadiceum (53: +), Peltigera rufescens (53: +), Pohlia sp. (53: +), Polytrichum hyperboreum (53: +), Ptilidium ciliare (53: +), Pertusaria panyrga (57: 2), Didymodon spadiceus (57: 1), Baeomyces rufus (57: +), Lophozia excisa (57: +), Dactylina ramulosa (52: 2), Cladonia occifera (52: 1), Bryum sp. (52: +), Cladina stygia (52: +), Ditrichum flexicaule (52: +), Peltigera sp. (52: +), Polygonum bistorta var. plumosum (52: +), Pedicularis lapponica (52: r), Arctagrostis latifolia (54: +).

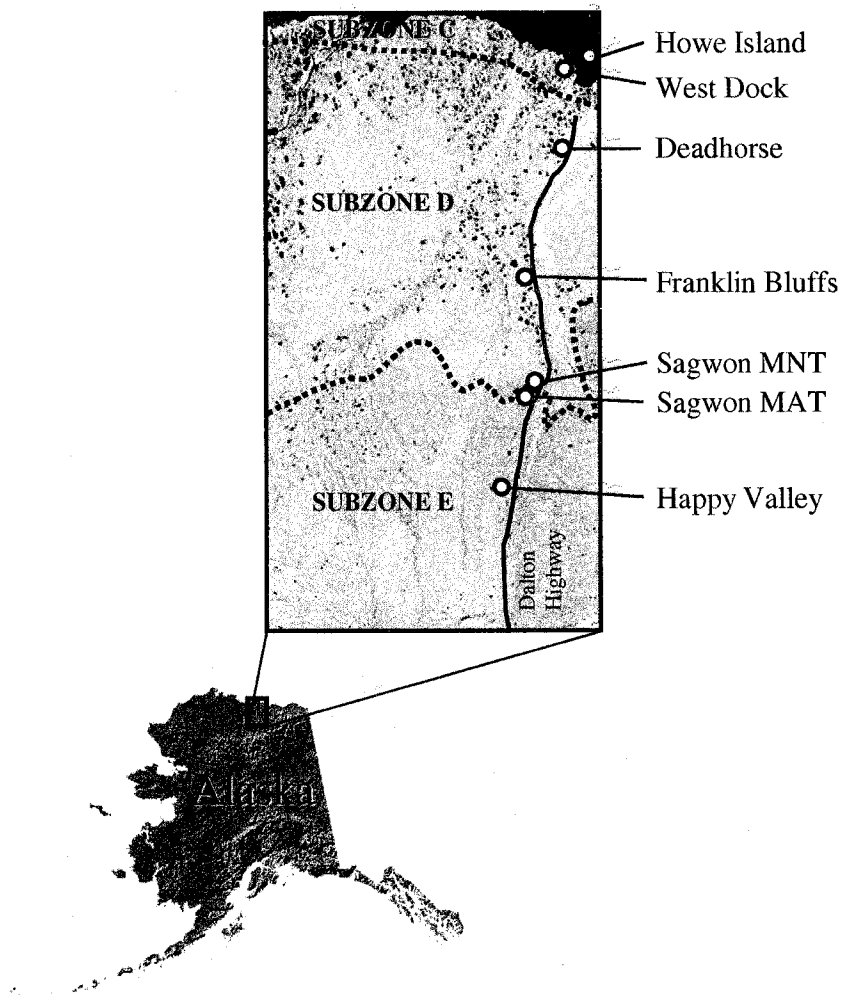

Fig. 2.1. Location of the three climatic subzones and the seven study sites along the northern segment of the Dalton Highway, Alaska.

Fig. 2.2. Nonsorted circles dominating the landscape at Howe Island, subzone C, Alaska.

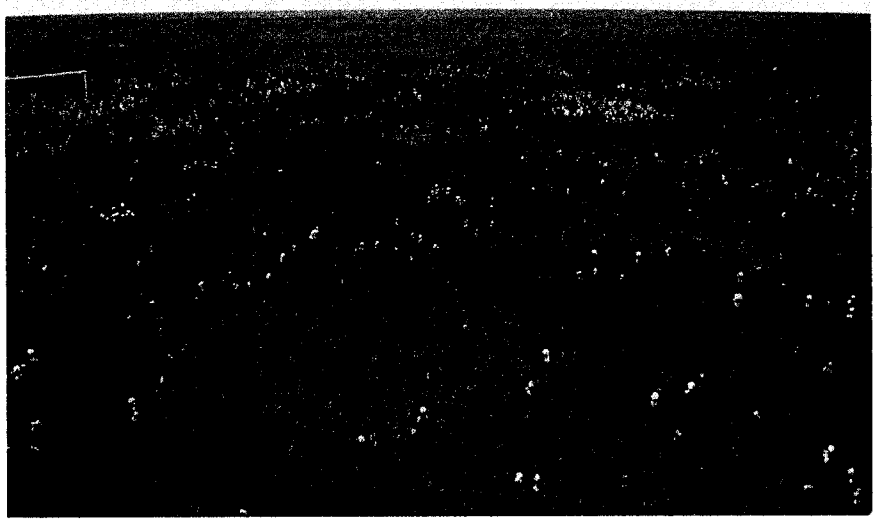

Fig. 2.3. Vegetated nonsorted circles at Deadhorse, subzone D, Alaska.

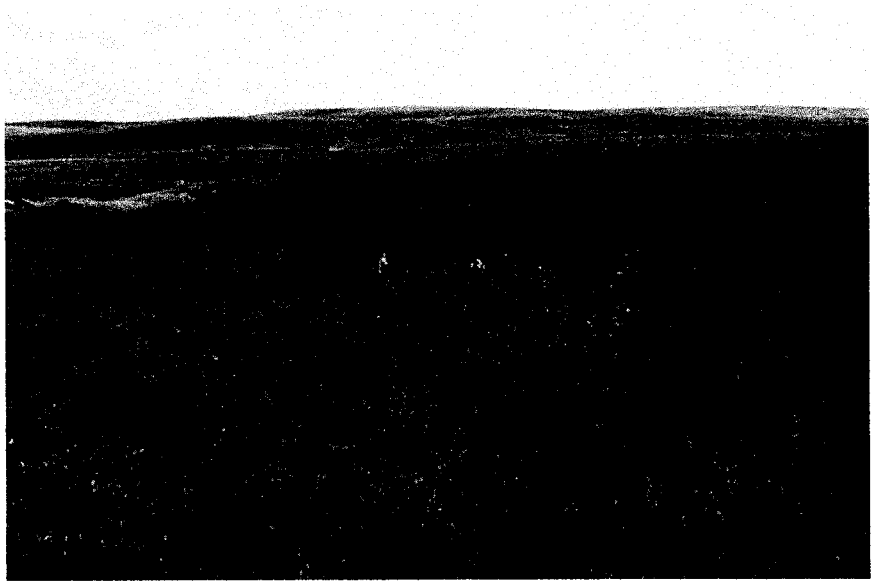

Fig. 2.4. Tussock tundra at Happy Valley, subzone E, Alaska.

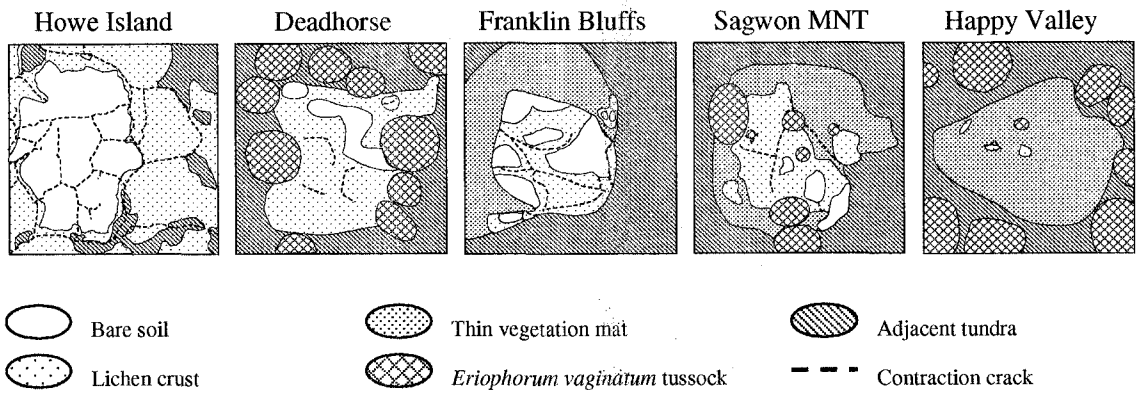

Fig. 2.5. Vegetation maps (1 m by 1 m) of nonsorted circles at several study sites along the bioclimate gradient from north to south.

Fig. 2.6. *Braya purpurascens-Puccinellia angustata* community, with the typicum variant occurring on the dry nonacidic nonsorted circles and the *Mycobilimbia lobulata* variant occurring on the small polygons surrounding the central bare area. Subzone C, Howe Island, Alaska.

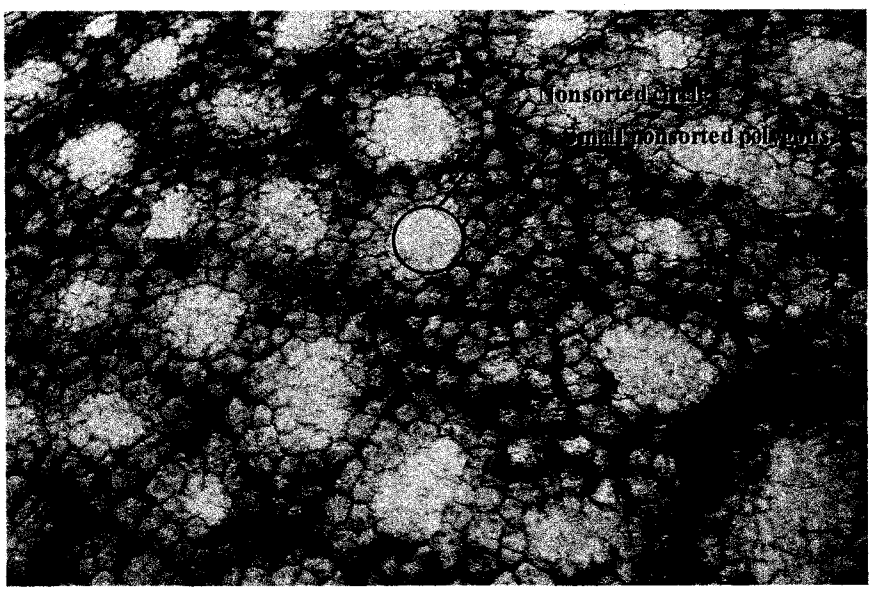

Fig. 2.7. Aerial view of a network of frost-heave features at Howe Island, Alaska. Note the small nonsorted polygons forming concentric rings around the nonsorted circles.

Fig. 2.8. *Dryas integrifolia-Salix arctica* community of the well-vegetated and stable, dry nonacidic tundra. Subzone C, Howe Island, Alaska.

Fig. 2.9. Salici rotundifoliae-Caricetum aquatilis ass. nov. as part of the moist nonacidic coastal tundra. Subzone C, West Dock, Alaska.

Fig. 2.10. Junco biglumis-Dryadetum integrifoliae bryetosum wrightii subass. nov. on barren, moist nonacidic nonsorted circles. Subzone D, Franklin Bluffs, Alaska.

Fig. 2.11. Junco biglumis-Dryadetum integrifoliae pedicularetosum subass. nov. on well-vegetated, moist nonacidic nonsorted circles. Subzone D, Franklin Bluffs, Alaska.

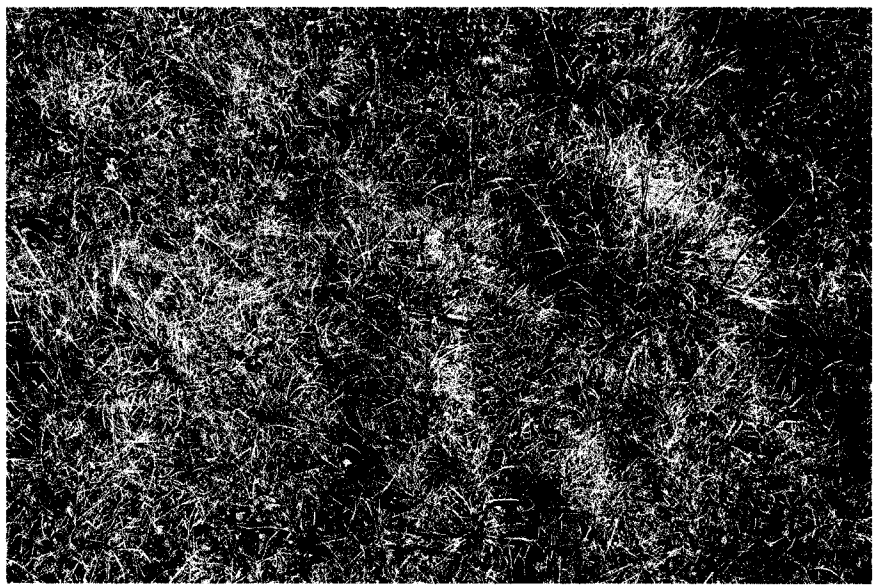

Fig. 2.12. Dryado integrifoliae-Caricetum bigelowii Walker *et al.* 1994 of the moist nonacidic tundra. Subzone D, Franklin Bluffs, Alaska.

Fig. 2.13. *Scorpidium scorpioides-Carex aquatilis* community of the wet nonacidic tundra. Subzone D, Franklin Bluffs, Alaska.

Fig. 2.14. Cladino-Vaccinietum vitis-idaeae ass. nov. on dry to moist nonsorted circles and earth hummocks of the acidic tundra. Subzone E, Happy Valley, Alaska.

Fig. 2.15. Sphagno-Eriophoretum vaginati Walker *et al.* 1994 of the moist acidic tundra. Subzone E, Sagwon MAT, Alaska.

Fig. 2.16. *Anthelia juratzkana-Juncus biglumis* community on relatively wet acidic frost boils. Subzone E, Happy Valley, Alaska.

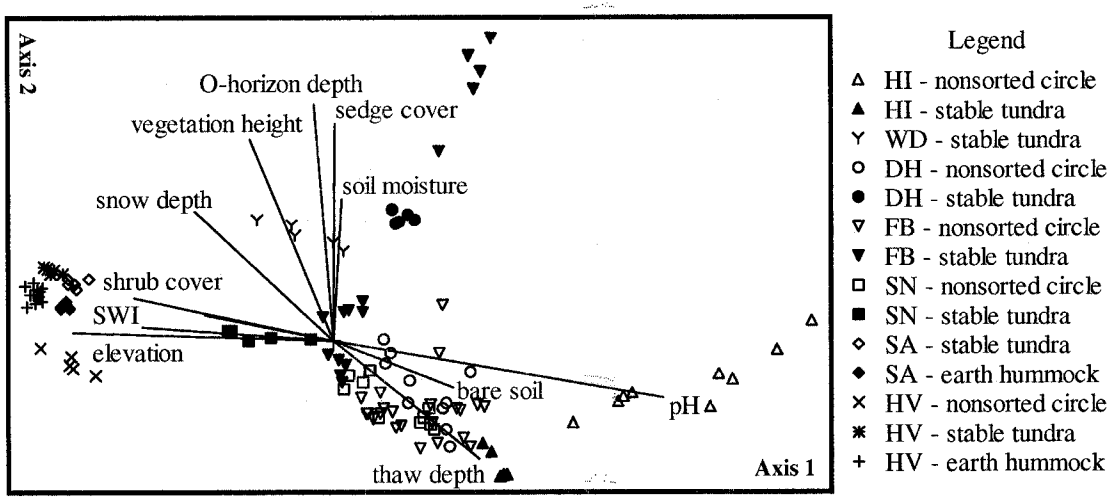

Fig. 2.17. DCA ordination of all relevés. The biplot diagram displays variables correlated with the plot distributions and indicates the direction and strength of correlation of variables with $R^2 > 0.35$. The sample plots are coded according to the location of the study sites: HI – Howe Island, WD – West Dock, DH – Deadhorse, FB – Franklin Bluffs, SN – Sagwon MNT, SA – Sagwon MAT, HV – Happy Valley.

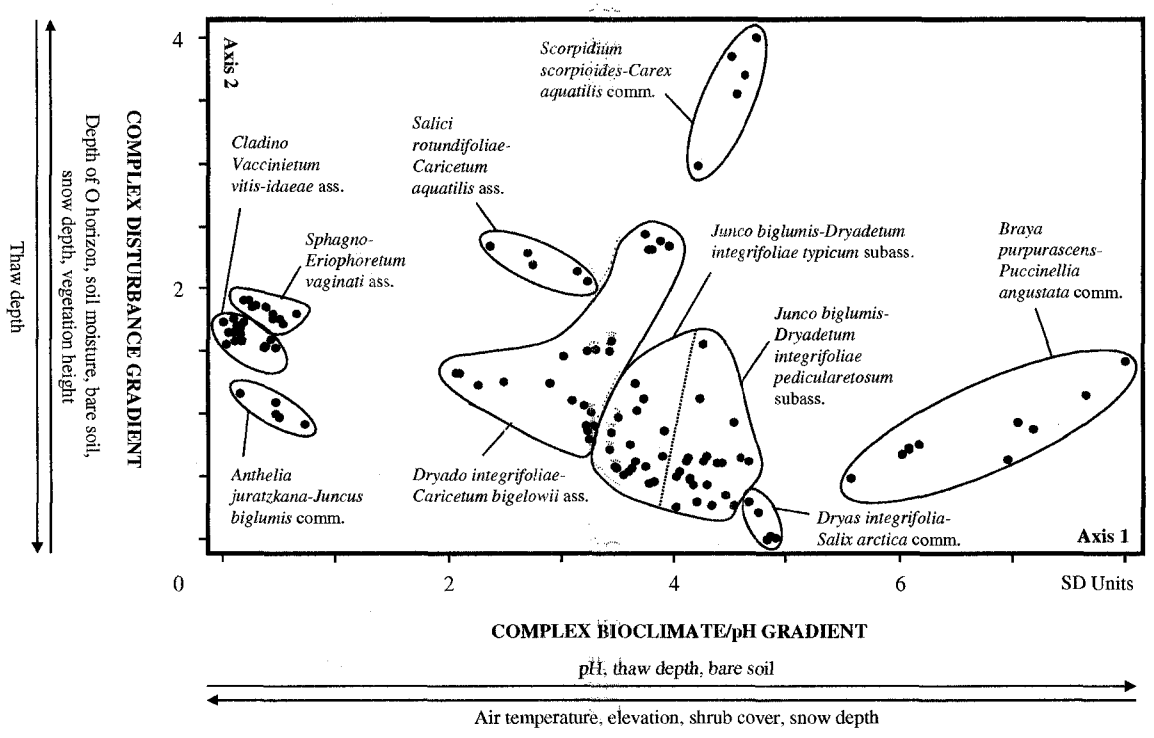

Fig. 2.18. DCA ordination of all relevés. The sample plots are grouped according to association or community. Arrows along each DCA axis indicate the direction of the principal environmental gradients. Axes are labeled in SD units (see text for interpretation).

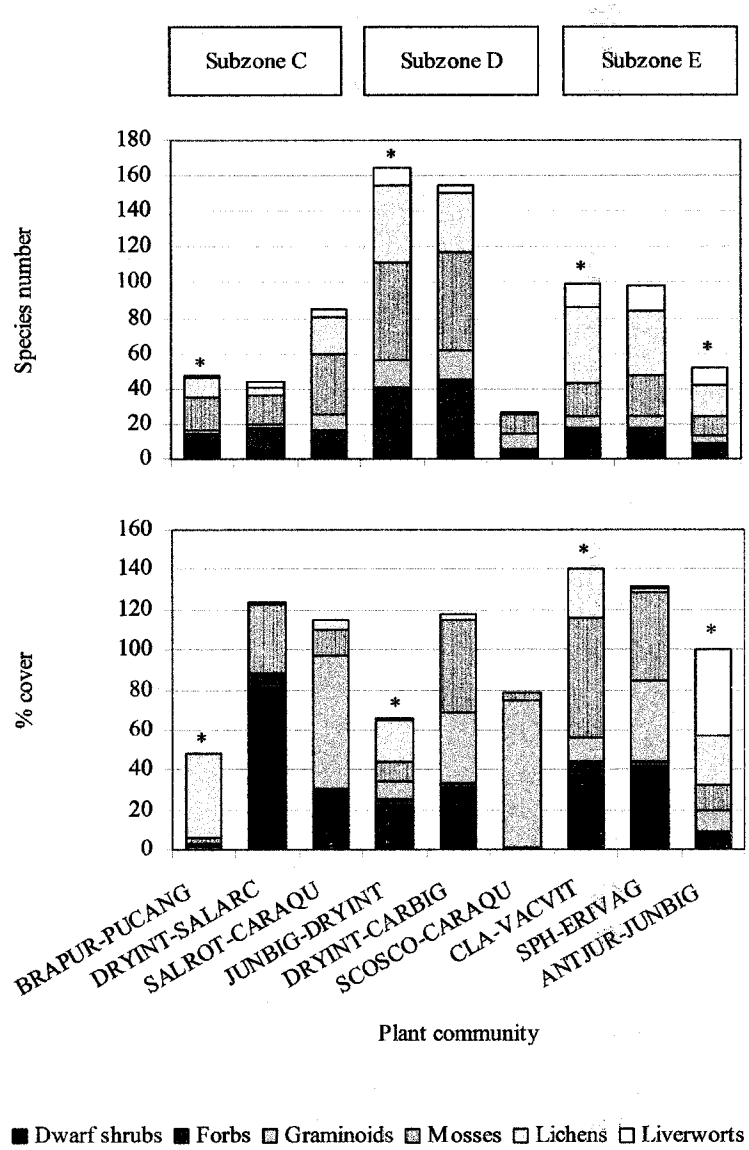

Fig. 2.19. Analysis of the species richness and plant functional types of the cryoturbated tundra communities. Plant functional types are shown as species numbers and percent cover values. Key to plant communities: BRAPUR-PUCANG = Braya purpurascens-Puccinellia angustata comm., DRYINT-SALARC = *Dryas integrifolia-Salix arctica* comm., SALROT-CARAQU = Salici rotundifoliae-Caricetum aquatilis, JUNBIG-DRYINT = Junco biglumis-Dryadetum integrifoliae, DRYINT-CARBIG = Dryado integrifoliae-Caricetum bigelowii, SCOSCO-CARAQU = *Scorpidium scorpioides-Carex aquatilis* comm., CLA-VACVIT = Cladino-Vaccinietum vitis-idaeae, SPH-ERIVAG = Sphagno-Eriophoretum vaginati, ANTJUR-JUNBIG = *Anthelia juratzkana-Juncus biglumis* comm. Plant communities associated with cryoturbation activity are marked with *.

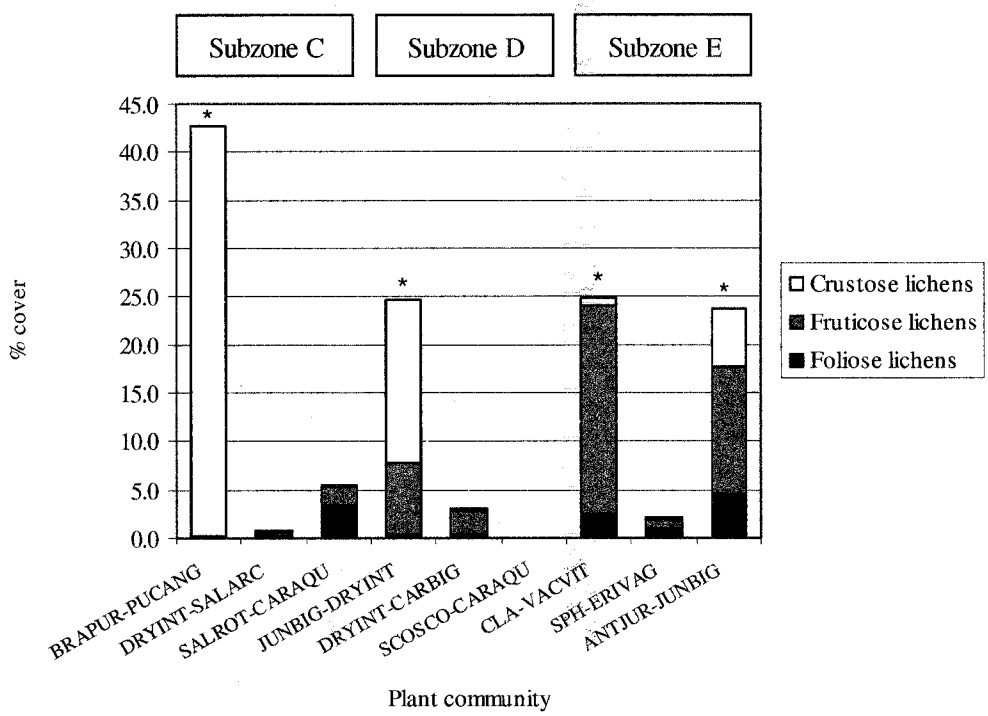

Fig. 2.20. Analysis of lichen cover of the cryoturbated tundra communities based on their growth form. See Fig. 2.19 for key to plant communities.

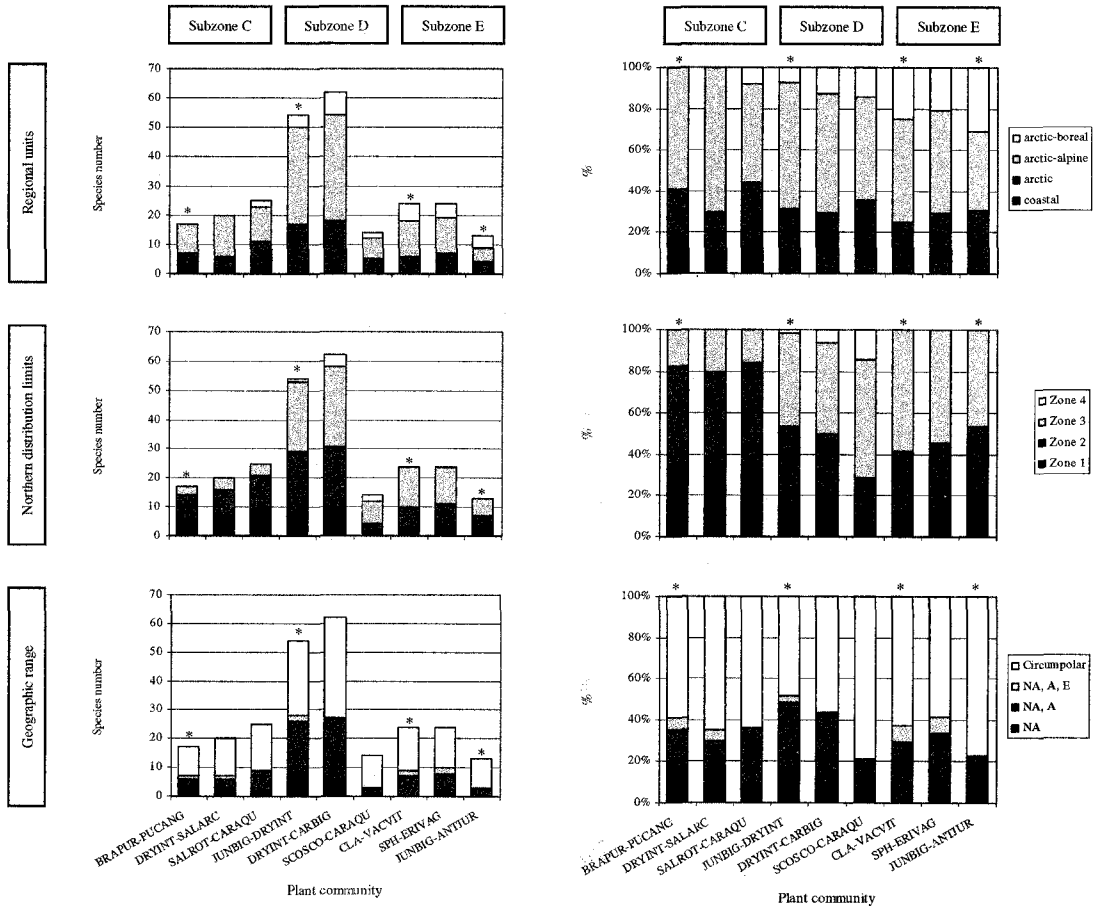

Fig. 2.21. Floristic analysis for vascular species of the cryoturbated tundra communities. The major regional units, northern distribution limits and geographic ranges are shown as total species numbers and percent values. See Fig. 2.19 for key to plant communities. Key to geographic range units: NA = North America, A = Asia, E = Europe.

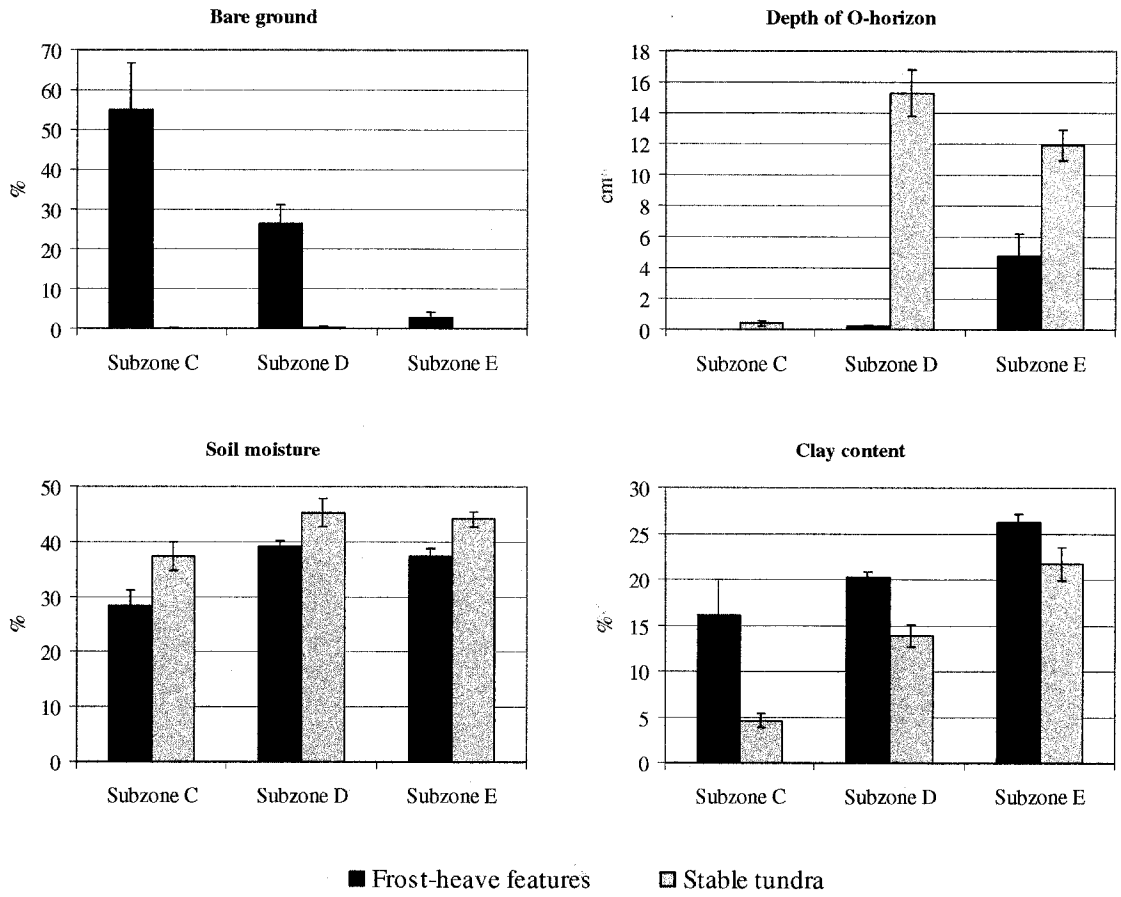

Fig. 2.22. Soil physical properties of frost-heave features and adjacent stable tundra sites for the different climatic subzones. Means and standard errors for the cover of bare ground, depth of the organic horizon, volumetric soil moisture and clay content are shown.

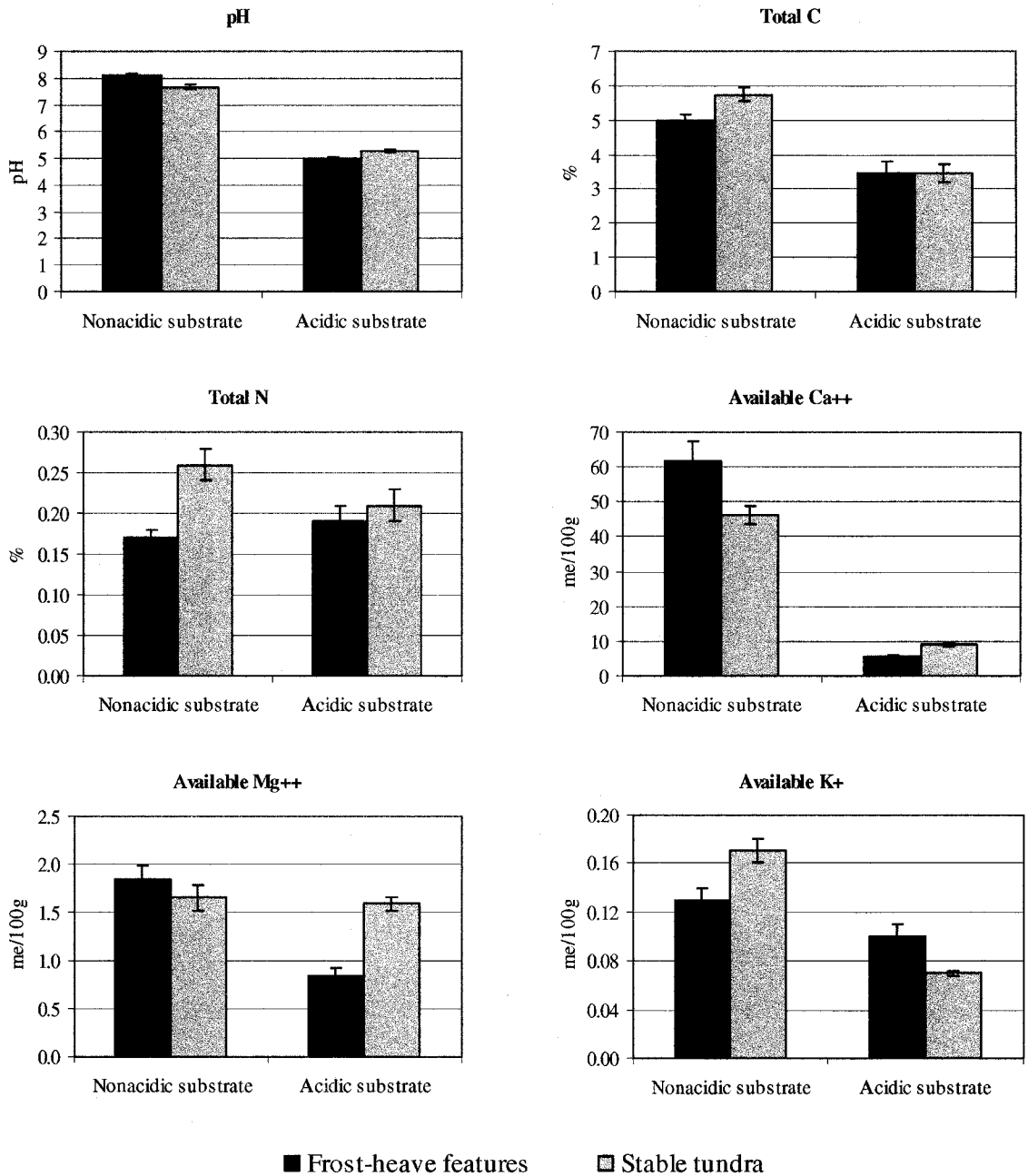

Fig. 2.23. Soil chemical properties of frost-heave features and stable tundra sites on nonacidic and acidic substrates. Means and standard errors for pH, total C, total N, available Ca^{2+}, available Mg^{2+} and available K^{+} are shown.

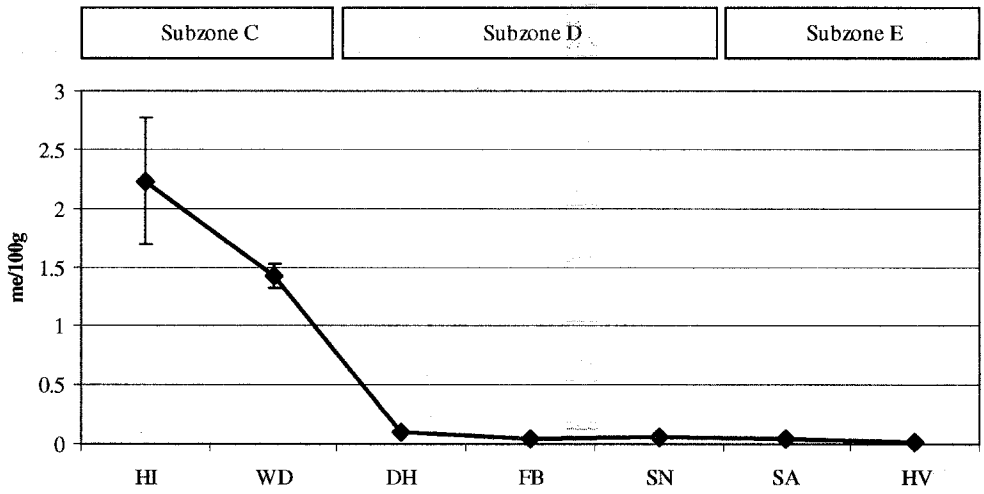

Fig. 2.24. Available Na^+ of the mineral soils of the cryoturbated tundra. Means and standard errors are shown for each study site, which are listed from north to south. See Fig. 2.17 for key to the study sites.

APPENDIX 2.1. Synoptic table of all vegetation communities. Species occurring in only one community type with constancy <II are omitted. Key to reference numbers: 1 *Braya purpurascens-Puccinellia angustata* comm., 2 *Dryas integrifolia-Salix arctica* comm., 3 Salici rotundifoliae-Caricetum aquatilis, 4 Junco biglumis-Dryadetum integrifoliae, 5 Dryado integrifoliae-Caricetum bigelowii, 6 *Scorpidium scorpioides-Carex aquatilis* comm., 7 Cladino-Vaccinietum vitis-idaeae, 8 Sphagno-Eriophoretum vaginati, 9 *Anthelia juratzkana-Juncus biglumis* comm.

Reference No.	1	2	3	4	5	6	7	8	9
Number of relevés	10	5	5	42	20	5	15	10	5
D Braya purpurascens-Puccinellia angustata comm.									
Braya glabella ssp. purpurascens	V^{1}	III	.	r^{+}	.	.	.	.	.
Fulgensia bracteata	V^{+}	.	.	.	.	.	.	.	.
Puccinellia angustata	V^{+}	.	.	.	.	.	.	.	.
Mycobilimbia lobulata	IV^{3}	.	.	I^{+}	r^{+}	.	.	.	.
Polyblastia bryophila	IV^{2}	.	.	.	.	.	.	.	.
Hennediella heimii var. arctica	IV^{1}	.	.	.	.	.	.	.	.
Potentilla uniflora	II^{+}	.	.	.	.	.	.	.	.
D Dryas integrifolia-Salix arctica comm.									
Salix ovalifolia	III^{+}	V^{2}	II^{2}	.	.	.	.	.	.
Ctenidium procerrimum	II^{+}	V^{2}	.	r^{+}	+$^{+}$	.	.	.	.
Chrysanthemum integrifolium	II^{+}	V^{1}	.	III^{+}	+	.	.	.	.
Festuca baffinensis	.	V^{+}	.	.	.	.	.	.	.
Cerastium beeringianum	II^{+}	V^{+}	.	.	.	.	.	.	.
Melandrium apetalum	.	V^{+}	I^{+}	r^{+}	.	.	.	.	.
Stellaria longipes	.	V^{+}	II^{+}	.	+$^{+}$	.	.	.	.
Tortula ruralis	II^{+}	IV^{1}	.	r^{+}	.	.	.	.	.
Artemisia campestris ssp. borealis var. borealis	I	IV^{+}	.	.	.	.	.	.	.
Didymodon asperifolius	.	III^{+}	.	.	.	.	.	.	.
Abietinella abietina	.	II^{1}	.	.	r^{+}	.	.	.	.
D Salici rotundifoliae-Caricetum aquatilis									
Salix rotundifolia	.	.	V^{2}	.	.	.	.	.	.
Nephroma expallidum	.	.	IV^{2}	.	r	.	I^{+}	II^{+}	.
Cladonia pyxidata	.	.	IV^{+}	+$^{+}$	II^{+}	.	I^{+}	.	.
Poa arctica	.	.	IV^{+}	.	r^{+}	.	.	.	.
Saxifraga cernua	.	.	III^{+}	.	.	.	.	.	.
Dicranum majus	.	.	III^{+}	.	.	.	.	.	.
Myurella tenerrima	.	.	III^{+}	.	.	.	.	.	.
Sanionia uncinata	.	.	III^{+}	r^{2}	.	.	.	.	.
Polytrichastrum alpinum	.	.	II^{1}	.	.	.	.	+$^{+}$	.
Cladonia ecmocyna	.	.	II^{+}	.	.	.	.	.	.
Cladonia furcata	.	.	II^{+}	.	.	.	.	.	.
Lecidea ramulosa	.	.	II^{+}	.	.	.	.	.	.
D Junco biglumis-Dryadetum integrifoliae									
Cladonia pocillum	.	.	II^{+}	V^{+}	II^{+}	.	.	+$^{+}$	.
Carex capillaris	.	.	.	IV^{+}	I^{+}	.	.	.	.
Aneura pinguis	.	I^{+}	II^{+}	IV^{+}	.	I^{+}	.	+$^{+}$	.
Solorina bispora	.	.	I^{+}	IV^{+}	I^{+}	.	.	.	.
Senecio resedifolius	.	.	.	III^{+}	+$^{+}$	.	.	.	.
Bryum wrightii	.	.	.	III^{+}	.	.	.	.	.
Vulpicida tilesii	.	.	.	II^{1}	r^{+}	.	.	.	.
Antennaria friesiana	.	.	.	II^{+}	r^{+}	.	.	.	.
Juncus triglumis	.	.	.	II^{+}	.	.	.	.	.
Minuartia rossii	.	.	.	II^{+}	.	.	.	.	.
Hymenostylium recurvirostre	.	.	.	II^{+}	.	.	.	.	.
Nostoc commune	.	.	.	II^{+}	.	.	.	.	.
D Dryado integrifoliae-Caricetum bigelowii									
Carex bigelowii	.	.	I^{1}	.	V^{2}	III^{+}	III^{2}	III^{1}	.
Salix reticulata	.	.	II^{1}	III^{1}	V^{2}	.	.	.	.
Arctostaphylos rubra	.	.	.	II^{+}	IV^{2}	.	+^{2}	.	.
Papaver macounii	.	.	.	I^{+}	IV^{+}	.	.	.	.
Saussurea angustifolia	.	.	.	+$^{+}$	III^{+}	.	.	+$^{+}$	.
Carex vaginata	.	.	.	.	II^{+}	.	.	.	.

Oxytropis maydelliana	.	.	.	r+	II+	.	.	.	.
Pedicularis langsdorfii	.	.	.	r+	II+	.	.	.	.
Saxifraga hieracifolia	.	.	.	.	II+	.	.	.	.
D Scorpidium scorpioides-Carex aquatilis comm.									
Pedicularis sudetica ssp. albolabiata	.	.	II-	.	II+	V1	.	.	.
Carex saxatilis	.	.	.	.	.	IV+	.	.	.
Pedicularis parviflora	.	.	.	.	.	II+	.	.	.
Limprichtia cossonii	.	.	.	.	.	II+	.	.	.
D Cladino-Vaccinietum vitis-idaeae									
Cladina arbuscula	.	.	.	.	.	.	V2	III+	.
Racomitrium lanuginosum	.	.	.	.	.	.	IV2	.	.
Dicranum spadiceum	.	.	I+	.	II+	.	IV1	I+	I-
Cladonia uncialis	.	.	I+	.	.	.	III1	+-	I-
Pertusaria dactylina	I+	.	.	.	.	.	III+	+-	.
Polytrichum hyperboreum	.	.	.	.	.	.	III+	.	I+
Rubus chamaemorus	.	.	.	.	.	.	II2	.	.
Cladonia gracilis ssp. elongata	.	.	.	.	.	.	II1	.	.
Cladonia cenotea	.	.	.	.	.	.	II+	+-	.
Lophozia ventricosa	.	.	.	.	.	.	II+	.	.
D Sphagno-Eriophoretum vaginati									
Salix planifolia ssp. pulchra	.	.	III1	.	.	.	I1	V2	II
Sphagnum warnstorfii	.	.	.	.	.	.	.	V2	.
Sphagnum angustifolium	.	.	.	.	.	.	.	IV2	.
Sphagnum girgensohnii	.	.	.	.	.	.	.	IV2	.
Pedicularis lapponica	.	.	.	.	.	.	II+	IV+	I
Saxifraga nelsoniana	.	.	.	.	I+	.	.	III+	.
Cladonia cyanipes	.	.	.	.	.	.	+-	II+	.
Sphagnum balticum	.	.	.	.	.	.	.	II+	.
Tritomaria quinquedentata	.	.	.	.	r+	.	.	II+	.
D Anthelia juratzkana-Juncus biglumis comm.									
Anthelia juratzkana	.	.	.	.	.	.	+-	.	V1
Dicranella subulata	.	.	.	.	.	.	.	.	V1
Luzula arctica	.	.	.	.	.	.	I+	+-	III2
Cephalozia bicuspidata	.	.	.	+-	.	.	.	+-	III+
Jungermania confertissima	.	.	.	.	.	.	.	.	III+
Lophozia sudetica var. sudetica	.	.	.	.	.	.	.	.	II+
Pohlia cruda	.	.	.	.	.	.	.	.	II+
Didymodon spadiceus	.	.	.	r+	.	.	.	.	I1
D Carici rupestris-Kobresietea bellardii: Dryadion integrifoliae									
Dryas integrifolia	+-	V4	IV2	V2	V2	I	.	.	.
Hypnum bambergeri	.	II+	II+	IV1	IV1	.	.	.	.
Minuartia arctica	.	IV+	I+	II1	III+	.	.	.	.
Saxifraga oppositifolia	+-	V1	.	V1	II+	.	.	.	.
Pedicularis capitata	I	V+	.	II+	IV+	.	.	+-	.
Carex rupestris	.	I	.	II+	I+	.	.	.	.
Lloydia serotina	.	I+	.	I+	.	.	.	.	.
Pedicularis kanei	.	.	.	III+	IV+	.	I+	.	.
Tofieldia pusilla	.	.	.	IV+	II+	.	.	.	.
Carex scirpoidea	.	.	.	II+	II+	.	.	.	.
Silene acaulis	.	.	.	I1	II+	.	.	.	.
Rhododendron lapponicum	.	.	.	I1	+-	.	.	.	.
Kobresia myosuroides	.	.	.	r+	I1	.	.	.	.
D Scheuchzerio-Caricetea nigrae									
Carex aquatilis	.	.	V3	.	r+	IV+	.	.	.
Campylium stellatum	I-	III+	IV+	III+	II1	III-	.	.	.
Equisetum variegatum	.	.	I+	III+	IV+	V+	.	.	.
Eriophorum angustifolium ssp. triste	.	.	V2	V1	V3	.	.	.	.
Bryum pseudotriquetrum	.	I+	IV+	I+	II+	.	.	.	.
Limprichtia revolvens	.	.	IV+	.	I+	.	.	.	.
Hierochloe pauciflora	.	.	III+	.	.	.	.	.	.
Saxifraga hirculus	.	.	III+	.	.	.	.	.	.
Oncophorus wahlenbergii	.	.	II2	.	.	.	.	.	.
Cinclidium arcticum	.	.	II+	+-	I+	.	.	.	.
Cinclidium latifolium	.	.	II+	.	.	.	.	.	.
Dupontia fisheri	.	.	II+	.	.	.	.	.	.
Eriophorum angustifolium ssp. subarcticum	.	.	.	I1	II3	V4	.	.	.
Scorpidium scorpioides	.	.	.	.	+-	V1	.	.	.
Carex atrofusca	.	.	.	r1	+-	III+	.	.	.
Carex rariflora	.	.	.	.	.	II+	.	.	.

D Loiseleurio-Vaccinietea																									
Betula nana	.	.	.	.	.	.																	V^{2}	V^{2}	V^{+}
Ledum palustre ssp. decumbens	.	.	.	.	.	.																	V^{2}	V^{2}	V^{1}
Vaccinium vitis-idaea	.	.	.	.	r^{+}	.																	V^{2}	V^{2}	V^{1}
Flavocetraria cucullata	.	.	II^{+}	IV^{1}	IV^{1}	.																	V^{1}	V^{+}	III^{2}
Dicranum elongatum	.	.	I^{+}	.	I^{2}	.																	V^{2}	IV^{1}	.
Empetrum nigrum ssp. hermaphroditum	.	.	.	.	+	.																	IV^{2}	IV^{2}	III^{+}
Cladonia amaurocraea	.	.	I^{+}	r	I^{+}	.																	IV^{+}	IV^{+}	III^{+}
D Non-sorted circles																									
Lecanora epibryon	III^{1}	I^{+}	.	IV^{1}	.	.																	.	.	.
Polyblastia sendtneri	IV^{2}	.	.	IV^{2}	.	.																	.	.	.
Juncus biglumis	+$^{+}$	.	.	IV^{+}	.	.																	.	.	III^{+}
D Subzone C and non-sorted circles in subzone D																									
Androsace chamaejasme	II^{+}	III^{+}	.	r^{+}	.	.																	.	.	.
Lophozia collaris	I^{+}	II^{+}	.	II^{+}	.	.																	.	.	.
Rinodina roscida	+$^{+}$	II^{+}	.	II^{+}	.	.																	.	.	.
Orthothecium varia	II^{+}	I^{+}	.	r^{+}	.	.																	.	.	.
D Nonacidic tundra																									
Distichium capillaceum	+$^{+}$	III^{2}	III^{2}	V^{1}	IV^{1}	III^{+}	.	.	.																
Salix arctica	+$^{+}$	V^{2}	V^{1}	III^{+}	IV^{2}	V^{+}	.	+$^{+}$	.																
Polygonum viviparum	+$^{+}$	V^{+}	III^{+}	V^{+}	V^{+}	.	.	.	.																
Distichium inclinatum	II^{1}	II^{2}	II^{+}	II^{+}	II^{1}	.	.	.	.																
Didymodon rigidulus var. icmadophilus	+$^{+}$	I^{+}	.	r^{+}	+$^{+}$	.	.	.	.																
Cirriphyllum cirrosum	I^{+}	.	I^{+}	II^{+}	II^{+}	.	.	.	.																
Ochrolechia frigida	+	.	II^{+}	II^{1}	r	.	.	.	.																
Bryoerythrophyllum recurvirostre	I^{+}	.	II^{1}	r^{+}	r^{+}	.	.	.	.																
Cochlearia officinalis	II^{+}	III^{+}	I	.	.	.	.	.	.																
Encalypta alpina	I^{1}	.	.	II^{+}	I^{+}	.	.	.	.																
Meesia uliginosa	.	.	II^{+}	II^{+}	+$^{+}$	I^{+}	.	.	.																
Pseudocalliergon turgescens	.	.	I^{+}	r^{+}	I^{+}	I^{+}	.	.	.																
Orthothecium chryseum	.	.	II^{+}	II^{+}	III^{1}	.	.	.	.																
Drepanocladus brevifolius	.	.	I^{1}	r^{+}	II^{2}	.	.	.	.																
Aulacomnium acuminatum	.	.	I^{+}	r^{1}	II^{1}	.	.	.	.																
Carex misandra	.	.	I^{+}	+$^{+}$	+$^{+}$	.	.	.	.																
Caloplaca tiroliensis	.	.	I^{+}	+$^{+}$	r^{+}	.	.	.	.																
Catoscopium nigritum	.	.	.	II^{+}	II^{1}	III^{+}	.	.	.																
Equisetum arvense	.	.	.	III^{1}	II^{+}	I	.	.	.																
Salix lanata ssp. richardsonii	.	.	.	r^{+}	III^{2}	II^{+}	.	.	.																
Orthothecium strictum	.	.	.	II^{+}	I^{+}	I^{+}	.	.	.																
Carex membranacea	.	.	.	IV^{1}	V^{1}	.	.	.	.																
Cardamine hyperborea	.	.	.	IV^{+}	IV^{+}	.	.	.	.																
Astragalus umbellatus	.	.	.	III^{+}	II^{1}	.	.	.	.																
Parrya nudicaulis	.	.	.	II^{+}	III^{+}	.	.	.	.																
Lupinus arcticus	.	.	.	I^{1}	II^{1}	.	.	.	.																
D Moist tundra																									
Cetraria islandica	.	.	V^{+}	IV^{+}	IV^{+}	.	III^{+}	III^{+}	IV^{+}																
Dactylina arctica	.	.	V^{+}	II^{+}	IV^{+}	.	V^{+}	V^{+}	III^{+}																
Peltigera leucophlebia	.	.	I^{1}	r^{+}	+$^{+}$	.	IV^{1}	III^{+}	II^{2}																
Cladonia gracilis	.	.	II^{+}	r^{+}	I^{+}	.	I^{1}	+$^{+}$	II^{+}																
Blepharostoma trichophyllum	.	.	II^{+}	II^{+}	r^{+}	.	+$^{+}$	III^{1}	.																
Senecio atropurpureus	.	.	I^{+}	III^{+}	V^{+}	.	III^{+}	IV^{+}	.																
Peltigera aphthosa	.	.	II^{+}	r^{+}	I^{+}	.	II^{1}	II^{1}	.																
Aulacomnium palustre	.	.	III^{+}	r^{+}	r^{+}	.	+$^{+}$	II^{+}	.																
Cassiope tetragona	.	.	.	I^{+}	IV^{1}	.	V^{1}	V^{2}	IV^{1}																
Vaccinium uliginosum	.	.	.	r	II^{+}	.	I^{+}	II^{1}	III^{+}																
Pertusaria panyrga	.	.	.	I^{2}	I^{+}	.	II^{+}	+$^{+}$	I^{2}																
Alectoria nigricans	.	.	I^{+}	r^{+}	.	.	I^{+}	+$^{+}$	.																
Flavocetraria nivalis	.	.	.	III^{+}	III^{+}	.	II^{+}	I^{+}	.																
Rhytidium rugosum	.	.	.	I^{+}	III^{1}	.	II^{1}	+$^{+}$	.																
Hypogymnia subobscura	.	.	I^{+}	r^{+}	.	.	I^{+}	.	.																
Cladonia squamosa	.	.	I	r^{+}	.	.	+$^{+}$	.	.																
Polytrichum strictum	.	.	III^{+}	.	.	.	II^{+}	+$^{+}$	.																
Dicranum angustum	.	.	II^{+}	.	.	.	I^{+}	III^{1}	.																
Sphaerophorus globosus	.	.	I^{+}	.	.	.	I^{+}	I^{+}	.																
D Acidic tundra																									
Aulacomnium turgidum	.	.	I^{+}	r^{+}	II^{2}	.	V^{1}	V^{2}	III^{+}																
Cladina rangiferina	.	.	.	.	.	.	V^{2}	IV^{+}	III^{2}																
Polygonum bistorta var. plumosum	.	.	.	r^{+}	I^{+}	.	V^{2}	V^{1}	I^{+}																
Anastrophyllum minutum	.	.	.	.	+$^{+}$	.	IV^{1}	IV^{1}	II^{+}																
Cladina stygia	.	.	.	.	.	.	III^{1}	IV^{+}	I^{+}																

Cladonia fimbriata	.	.	.	.	r+	.	III+	II+	III+
Ptilidium ciliare	.	.	.	.	I1	.	II1	IV+	I+
Cladonia coccifera	.	.	.	.	r+	.	I+	++	I1
Petasites frigidus	.	.	.	.	.	.	IV2	V+	.
Dicranum acutifolium	.	.	.	r+	r+	.	III+	III1	.
Pleurozium schreberi	.	.	.	.	r+	.	III1	III+	.
Cetraria laevigata	.	.	.	.	++	.	II+	III+	.
Peltigera scabrosa	.	.	.	.	++	.	II+	III+	.
Dicranum groenlandicum	.	.	.	.	.	.	II2	II1	.
Cladonia gracilis ssp. vulnerata	.	.	.	.	.	.	II1	II+	.
Cladonia deformis	.	.	.	.	.	.	II+	II+	.
Pedicularis labradorica	.	.	.	.	.	.	II+	II+	.
Pedicularis oederi	.	.	.	.	.	.	II+	II+	.
Peltigera malacea	.	.	.	.	r+	.	II+	II+	.
Salix phlebophylla	.	.	I+	.	.	.	II1	I+	.
Barbilophozia binsteadii	.	.	.	.	.	.	I+	II+	.
Hypnum holmenii	.	.	.	.	.	.	I+	II+	.
Nephroma arcticum	.	.	.	.	.	.	I+	II+	.
Cladonia chlorophaea	.	.	.	.	.	.	III+	.	II1
Cladina mitis	.	.	.	.	.	.	II2	.	II+
Lophozia excisa	.	.	.	.	.	.	I+	.	I+
Lophozia ventricosa	.	.	.	.	.	.	.	II+	II+
Other taxa									
Ditrichum flexicaule	++	V2	I+	V1	V1	III+	II+	II+	I+
Thamnolia subuliformis	II+	V+	V+	V1	V1	.	IV+	III+	.
Hylocomium splendens	.	IV+	IV+	++	II3	.	V2	V2	V1
Arctagrostis latifolia	+	.	.	III+	III+	.	IV2	II+	I+
Eriophorum vaginatum	.	.	.	III1	IV2	IV+	II1	V3	V1
Tomentypnum nitens	.	II1	IV1	IV1	V3	.	.	IV+	.

CHAPTER 3: THE MODIFIED N-FACTOR ALONG A CLIMATE GRADIENT IN PATTERNED-GROUND ECOSYSTEMS

[*] Submitted as: Kade A, Romanovsky VE, and Walker DA. 2005. The modified n-factor along a climate gradient in patterned-ground ecosystems. *Permafrost and Periglacial Processes* (submitted).

ABSTRACT

The vegetation and soil patterns in arctic tundra are influenced by the distribution of nonsorted circles, which are patterned-ground features caused by differential frost heave. This study used the modified n-factor (n'-factor), which is the ratio of the thawing degree-day sums at the soil surface to that in the air, to examine the insulative effect of vegetation and soil organic horizons on mineral soils in the summer, and the insulative effect of snow in the winter.

Three study sites were selected in bioclimate subzones C, D and E in Arctic Alaska. Air and mineral-soil surface temperatures of nonsorted circles and adjacent stable tundra plots were monitored from September 2003 through September 2004, and the thickness of the vegetation and soil organic horizons was measured. The summer and winter n'-factors were determined, and the Stefan solution was used to predict thaw depth.

The n'-factor is greater for nonsorted circles than for the adjacent tundra, and it decreases along a climate gradient from north to south. Thaw depth predictions using the Stefan solution are relatively accurate in subzone D and E but overestimate the actual values in subzone C. Increased vegetation growth and snow depth due to global warming might decrease the n'-factor and active-layer depth in northern areas in the future, and the morphological differences between nonsorted circles and the surrounding tundra might become less pronounced, particularly in the transitional areas between subzones D and E.

INTRODUCTION

Nonsorted circles are patterned-ground features measuring 0.5 to 3 m across that dominate the landscape in many arctic tundra regions (Washburn, 1980). Compared to the surrounding tundra areas, these cryogenic features typically have no or little vegetation cover and deeper thaw depths (Walker *et al.*, 2004; Kade *et al.*, 2005). Nonsorted circles are caused by differential frost heave that occurs when ice lenses form in soils during winter. The soils within the nonsorted circles heave more than in the surrounding tundra due to a deeper active layer and more ice lenses formed in the barren circles as a result of migration of water from the inter-circle areas (Peterson and Krantz, 2003). Nonsorted circles display tight linkages between thaw depth, frost heave and the minimal insulation provided by the thin vegetation mat and soil organic horizons (Walker *et al.*, 2004).

The active layer of the soil, the zone above the permafrost table that thaws annually, is a focus of much research in arctic ecosystems because changes in the thickness of this layer due to climate or anthropogenic causes have major implications for the entire ecological and geophysical system. Predicting the depth of thaw in the light of global climate change has been the topic of many studies (e.g., Nelson *et al.*, 1997; Romanovsky and Osterkamp, 1997; Hinzman *et al.*, 1998; Nelson *et al.*, 1998; Klene *et al.*, 2001). So far, most regional studies of active-layer distribution have examined mainly the effects of broad-scale changes to climate and vegetation patterns, and the regional significance of micro-scale features, such as nonsorted circles, has received little attention.

Several studies have investigated the cooling effect of vegetation on soil temperatures in the summer and the warming effect in winter (Beringer *et al.*, 2001; Pavlov and Moskalenko, 2002); yet no research to date has compared the insulative effect of different vegetation types with respect to cryogenic processes. Here, we focus on the influence of vegetation types on mineral soil-surface temperatures and thaw depth at a microscale, distinguishing between nonsorted circles and the surrounding stable tundra.

The energy balance at the soil surface is a major factor influencing the development of nonsorted circles (Peterson and Krantz, 1998; Peterson *et al.*, 2003); however, it is difficult to determine due to the interaction of several energy fluxes. The n-factor is a simple indicator of the energy balance at the soil surface, and it has been used in arctic engineering to estimate bare soil-surface temperatures of homogeneous artificial surfaces from air temperatures. The index is a quantitative measure of the interacting components of the energy balance at the ground surface, and it is defined as the ratio of seasonal thawing degree-day sums (TDD) at the soil surface to that in the air (Carlson, 1952). The degree-day based n-factor was developed in arctic engineering studies due to the strong relationship between TDD at the ground surface and the active-layer depth (Hildebrand, 1983).

Recently, the n-factor has been calculated for natural systems to assess the surface thermal regime under a variety of natural vegetation types (Klene *et al.*, 2001; Taylor, 2001), and to estimate permafrost temperatures and active-layer thickness over large areas (Smith and Riseborough, 1996; Klene *et al.*, 2001). However, the original concept of the n-factor is problematic when considering natural landscapes, as the energy balance

for areas with smooth paved surfaces of construction sites differs greatly from heterogeneous vegetated areas. It is difficult to define the physical surface of the vegetation layer, and the heat exchange in the vegetation and underlying soil organic horizon is complex. The n-factor for natural landscapes incorporates both the radiation balance at the soil surface as well as the insulative effect of the vegetation, soil organic horizon and snow.

The term "soil surface" needs to be defined when dealing with different plant canopy types and the presence of soil organic horizons. Here, we compare the air temperature to (a) the temperatures just below the living vegetation and (b) to the temperatures below the soil organic horizon at the mineral soil surface. This modified n-factor (n'-factor) presented in this study differs from the original concept developed by arctic engineers, and it is site-specific as it depends on the thickness and the type of the vegetation present and the snow cover during the winter.

The main purpose of this research is to show the insulative effect of the live vegetation and the soil organic horizon (dead vegetative matter) on the mineral soil thermal regime in the summer, and the insulative effect of vegetation, soil organic horizon and snow in the winter. The n'-factor was determined during the summer and the winter for plots with varying degrees of cryogenic activity and plant cover and then compared along a bioclimatic gradient. The n'-factor is less than one when the soil temperature is lower than the air temperature, indicating great thermal insulation of the soil organic layer. The n'-factor is close to one when the soil-surface and air temperatures are similar, and the n'-factor can reach values above one when the soil surface is warmer

than the air. Thus, the n'-factor should be greater for the poorly-insulated bare soils of the nonsorted circles than for the stable tundra soils under thick vegetation mats.

Measuring thaw depths over large areas is very labor-intensive, and some studies have used information from the n'-factor in the Stefan solution to estimate thaw depth (Carlson, 1952; Klene *et al.*, 2001). In this study, we establish the relationship between the summer n'-factor and thaw depth of the mineral soil at specific plots with known vegetation characteristics, and we compare the observed thaw-depth values of the mineral soil to the ones predicted by a basic version of the Stefan solution (Andersland and Ladanyi, 1994). The Stefan solution is named for the physicist Jožef Stefan, who introduced examples of phase boundary problems in the late 19th century. If the thaw-depth predictions are correct, linking the n'-factor to certain vegetation types and using this information in the Stefan solution will improve thaw-depth estimates over wide areas. In addition, the mean annual temperatures for air and the mineral soil surface are calculated to evaluate the annual net insulative effect of vegetation and snow on the mineral soil.

METHODS

Study area

The study was conducted along a bioclimate gradient from the coast of the Arctic Ocean to the Arctic Foothills along the northern segment of the Dalton Highway, Alaska (Fig. 3.1). From north to south, we investigated three study sites. Howe Island (Lat. 70° 18' N, Long. 147° 59' W, elevation 8 m asl) is a small island just north of the coast of the

Coastal Plain at Prudhoe Bay. According to the Circumpolar Arctic Vegetation Map (CAVM Team, 2003) and Walker (2000), Howe Island is part of bioclimate subzone C or the prostrate dwarf-shrub subzone, with mean July temperatures from 5 to 7°C. Farther south, Franklin Bluffs (Lat. 69° 40' N, Long. 148° 43' W, elevation 130 m asl) is located in the Arctic Coastal Plain, with many thaw lakes dotting the landscape. This site is classified as bioclimate subzone D or the erect dwarf-shrub subzone, with mean July temperatures from 7 to 9°C. The southernmost site is Happy Valley (Lat. 69° 08' N, Long. 148°50' W, elevation 315 m asl) in the Arctic Foothills, where rolling hills and broad valleys dominate the landscape. Happy Valley belongs to bioclimate subzone E or the low-shrub subzone, with mean July temperatures from 9 to 12°C. Both subzones C and D are part of the moist nonacidic tundra, and subzone E belongs to the moist acidic tundra. The climate of the area varies with distance from the Arctic Ocean and elevation. Temperature and precipitation increase from north to south. On the Arctic Coastal Plain, the mean annual precipitation ranges from 125 to 140 mm and 50% falls as snow. In the Arctic Foothills, mean annual precipitation ranges from 140 to 270 mm, with 40% falling as snow (Zhang *et al.*, 1996).

All sites are located in the zone of continuous permafrost (Péwé, 1975), and all soils experience frost heave due to ice-lens formation (Ping *et al.*, 1998; Walker *et al.*, 2003). Nonsorted circles are a common part of the landscape; however, the morphology of these frost-heave features changes along the bioclimatic gradient (Fig. 3.2). Large, almost barren nonsorted circles dominate the landscape on Howe Island. At Franklin Bluffs, the nonsorted circles are bare to slightly vegetated and smaller in diameter. At

Happy Valley, active nonsorted circles are very small and sparsely distributed, and most frost-heave features are less expressed due to thick vegetation mats.

Data collection

Frost-heave features typical for the area and adjacent stable tundra plots were selected at each study site. At Howe Island, five barren nonsorted circles and five stable tundra plots with typically thin vegetation mats were chosen. At Franklin Bluffs, ten barren to sparsely vegetated nonsorted circles, and ten stable tundra plots with intermediate to thick soil organic horizons were selected. At Happy Valley, five active, small barren nonsorted circles located between sedge tussocks, five less active and well-vegetated nonsorted circles, and five adjacent stable tundra plots were selected. At each study plot, one temperature logger (iButton, Maxim Integrated Products) was buried at 1-cm depth in the mineral soil to represent the "mineral soil surface", and it recorded soil temperatures every four hours during September 2003 until August 2004. In addition, one temperature logger was installed at the interface of the live vegetation and the soil organic horizon at well-vegetated study plots (Fig. 3.3). The sites are part of the permafrost observatory study sites (Osterkamp and Romanovsky, 1999), and air temperatures were recorded hourly with Campbell Scientific temperature monitoring systems. Also, air and soil-surface temperature data were recorded from 1999 to 2003 at Franklin Bluffs and used to investigate year-to-year variability in mean annual temperatures. The volumetric soil water content in the active layer of the mineral soil was recorded with a Hydra-Probe (Advanced Measurement and Control Company). At each

study plot, the thickness of the overlying live moss and vegetation mat and, if present, the soil organic horizon was recorded. The maximum snow depth and the overall snow density of each plot were measured in mid April 2004. In addition, one subjectively chosen representative snow profile was recorded at each study site. The maximum thaw depth of the mineral soil was measured in early September 2004 by pushing a rod through the active layer and subtracting the depth of the organic horizon.

Daily mean temperatures for the air, under the live vegetation and at the mineral soil surface were derived, and thawing degree-day sums for the air (TDD_a), live vegetation (TDD_v) and the mineral soil surface (TDD_m) were calculated by summing the daily mean temperatures from the first to the last day of the season that the mean soil-surface temperature rose above 0 °C. Similarly, the freezing degree-day sums were determined for the air (FDD_a), live vegetation (FDD_v) and the mineral soil surface (FDD_m) by summing the daily mean temperatures from the first to the last day of the season that the mean soil-surface temperature dipped below 0 °C. The following n'-factors were determined for each study plot (Fig. 3.3):

- Summer n'-factor for the live vegetation: $n'_v = TDD_v/TDD_a$
- Summer n'-factor at the mineral soil surface: $n'_m = TDD_m/TDD_a$
- Winter n'-factor for the live vegetation: $n'_v = FDD_v/FDD_a$
- Winter n'-factor at the mineral soil surface: $n'_m = FDD_m/FDD_a$

Data were analyzed using SAS (SAS Institute Inc., 2004). The environmental variables were compared between nonsorted circles and tundra plots performing univariate one-way analyses of variance, testing also for site interactions. A principal

component analysis (Hotelling, 1933) was performed to establish the multivariate relationships between the vegetation, n'-factor, thaw depth and other environmental variables. Data were standardized (mean = 0, variance = 1) to reduce the influence of variables with high variances. The thaw depth of the mineral soil was predicted by using a basic version of the Stefan solution (Andersland and Ladanyi, 1994), given by $z_t = [(2\ k_t\ s\ TDD_s)/(wL)]^{1/2}$, where z_t is the thaw depth of the mineral soil (m), k_t is the thermal conductivity of the thawed soil (1.2 W m^{-1} $°C^{-1}$ at Howe Island and Franklin Bluffs, 1.0 W m^{-1} $°C^{-1}$ at Happy Valley), s is a scaling factor (86,400 s d^{-1}), TDD_s is the thawing degree day sum at the soil surface (°C d), w is the volumetric soil water content expressed as a decimal proportion and L is the volumetric latent heat of fusion of water (334,000,000 J m^{-3}). The mean annual air temperature was determined for the three study sites for the hydrological year from September 2003 through August 2004. Similarly, the mean annual temperature at the mineral soil surface was determined for each study plot.

RESULTS AND DISCUSSION

Intrasite comparisons

Howe Island, subzone C

On Howe Island, the barren nonsorted circles had a very high summer n'_m-factor averaging 1.43 (Table 3.1), which is similar to the n-factor derived from paved asphalt surfaces. The unusually high n'_m-factor was likely the result of low air temperatures due to the proximity to the Arctic Ocean. Cool air temperatures from the ocean differed greatly from the soil-surface temperatures of the barren nonsorted circles, which absorbed

direct solar radiation and were considerably warmer. The summer n'_m-factor of the stable tundra was much lower (mean 0.99), where the 2-cm thick vegetation insulated the soil and resulted in similar soil and air temperatures. The summer n'_m-factor was correlated with maximum thaw depth of the mineral soil, which was deeper in the nonsorted circles (mean 81.2 cm, Fig. 3.4) than in the adjacent tundra (mean 62.6 cm). The soil water content of the upper mineral horizon was lower for the nonsorted circles (mean 25.4%) than for the surrounding tundra (mean 35.8%), where the vegetation layer apparently reduced evaporation.

Insulation of the soil surface due to the blanket of snow resulted in a lower n'_m-factor during the winter, and both nonsorted circles and stable tundra had similar winter n'_m-factors with means 0.94 and 0.87, respectively (Table 3.1). The maximum snow depth was shallower for the nonsorted circles (mean 5.8 cm, Fig. 3.4) than for the adjacent tundra (mean 11.0 cm), which can be explained by the effect of wind removing the snow from the heaved bare sites and vegetation trapping snow at the stable tundra plots. The nonsorted circles heaved about 5 cm more than the surrounding tundra, thus decreasing the distance from the ground surface to the surface of the snow layer. The stable tundra plots had deeper depth-hoar layers than the barren nonsorted circles (Table 3.2). The overall snow density was lower at the stable tundra (mean 0.30 g/cm^3) than at the nonsorted circles (mean 0.41 g/cm^3), which can be explained by the low density of the large and loosely packed depth-hoar crystals of the surrounding tundra.

Franklin Bluffs, subzone D

Most soils at Franklin Bluffs remained near saturation throughout the summer, slowing decomposition rates and resulting in thick soil organic horizons in the stable tundra. The summer n'-factor decreased with increasing depth of the vegetation and soil organic horizon. The mean summer n'_m-factor reached 0.97 at the relatively bare nonsorted circles, declining to 0.91 under about 8 cm of live vegetation and 0.35 under 21 cm thick organic horizons in the stable tundra (Table 3.1). The thaw depth of the mineral soil decreased with increasing vegetation and organic horizon thickness, averaging 93.6 cm for nonsorted circles and 46.1 cm for the stable tundra with thick organic horizons (Fig. 3.4). Soil water content was slightly lower at the nonsorted circles (mean 39.7%) than in the adjacent tundra (mean 45.1%).

The difference between the n'-factors of nonsorted circles and stable tundra plots decreased in the winter, with winter n'-factors ranging from 0.73 to 0.53 depending on snow depth and snow density (Table 3.1). The nonsorted circles had shallower snow with thinner depth-hoar layers and greater overall snow densities than the stable tundra plots (Fig. 3.4, Fig. 3.5). The difference in snow depth can be partly explained by differential frost heave during freeze-up, with the nonsorted circles heaving approximately 12 cm more than the adjacent tundra and thus resulting in shallower snow depth. The loosely packed depth-hoar crystals have very low thermal conductivity (Sturm *et al.*, 1997), and the deep snow and low snow density at the adjacent tundra insulated the soil surface, resulting in less negative soil than air temperatures and a lower winter n'-factor.

Happy Valley, subzone E

Farther south at Happy Valley, the small, active nonsorted circles were sparse and hidden under *Eriophorum vaginatum* tussocks. Shading from the tall surrounding vegetation and low position within the microrelief led to a relatively low summer n'_m-factor (mean 0.74, Table 3.1). The larger, less active nonsorted circles were covered by a relatively thick live vegetation mat and soil organic horizon (13 cm and 8 cm, respectively, Fig. 3.4), with the n'_v-factor averaging 0.89 and the n'_m-factor averaging 0.34 in the summer (Table 3.1). The surrounding tundra was characterized by tall tussocks and low shrubs, and the mean n'_v-factor was 0.76 and the mean n'_m-factor was 0.17 in the summer. The thaw depth of the mineral soil was greatest for the bare nonsorted circles and lowest for the surrounding tundra with means 59.5 cm and 21.0 cm, respectively (Fig. 3.4). Soil water content was greater in the stable tundra (mean 46.2%) than in the bare circles (mean 42.2%) and the vegetated circles (mean 38.8%).

The snow profiles were similar for nonsorted circles and the adjacent tundra, the major difference being the shallower depth-hoar layer of the nonsorted circles (Table 3.2). The stable tundra had deeper snow and lower snow densities (means 72.6 cm and 0.25 g/cm^3, Fig. 3.4) than the barren nonsorted circles (means 63.5 cm and 0.28 g/cm^3, respectively). However, the deeper snow depth at the stable tundra plots had only a minor additional warming effect on soil temperatures, and the winter n'-factor differed little among the plots, ranging from 0.32 to 0.41 (Table 3.1).

Intersite comparisons

At all sites, the bare nonsorted circles had significantly thinner live vegetation, soil organic mats and snow depths, and greater thaw depths and n'-factors than the adjacent stable tundra (Table 3.1). Several variables showed significant interactions between site and plot type: The differences in the thickness of the live vegetation and the summer n'_m-factor between circles and tundra increased towards the south, and the differences in the depth of the soil organic mat and thaw between circles and tundra were greatest at Franklin Bluffs in subzone D (Fig. 3.4 and Fig. 3.6). Along the climate gradient from north to south, summer temperatures and the thickness of the vegetation and soil organic horizon increased. Both the summer and winter n'_v-factor and n'_m-factor declined from north to south with increasing thickness of the live vegetation, soil organic horizon and snow and decreasing influence of the cool ocean air in the summer. From Howe Island to Happy Valley, the summer n'_m-factor decreased by about 50% for bare nonsorted circles and by about 80% for stable tundra plots. Shur and Borovskiy (1993) mapped n-factors in northern Russia and also found that the n-factor was greatest at the sea coast and declined inland towards more continental locations.

The thaw depth of the mineral soil was closely linked to the summer n'_m-factor and thickness of the overlying vegetation and soil organic horizons. The differences between n'_m-factors and thaw depths between bare nonsorted circles and the adjacent tundra increased towards the south, where very thick soil organic horizons overlay the stable tundra. The thaw depth of the barren nonsorted circles was greatest at Franklin Bluffs. At Howe Island, the cooler temperatures limited thaw depth of the mineral soil;

whereas at Happy Valley, the small nonsorted circles were shaded by the tall vegetation of the adjacent tundra.

The relationships among the thickness of the vegetation mat and soil organic horizon, summer and winter n'_m-factors, distance to the ocean as a measure of continentality, thaw depth, snow depth and density, and soil moisture for all study sites were identified in the principal component analysis (Table 3.3). The principal component analysis partitions variability and co-variability among several variables by forming uncorrelated linear combinations of the variables that explain decreasing amounts of variability. Here, the first principal component explained most variation of the data set (79%). It showed the great insulative effect of the vegetation mat and soil organic horizon on the mineral soil surface and on thaw depth, with negative loadings (Eigenvectors) of the thickness of the vegetation and organic horizon contrasting the positive loadings of the summer n'-factor and thaw depth. Similarly, the insulative effect of snow on the mineral soil surface was expressed in the negative loading of snow depth contrasting the positive loading of the winter n'_m-factor. This agrees with Pavlov and Moskalenko (2002), who estimated that a 0.2-m thick peat layer decreased the mineral soil-surface temperature of northwest Siberian tundra soils by 3.5 °C in the summer, and a 0.2-0.3-m thick snow cover increased the mineral soil-surface temperature by 4.3-4.5 °C in the winter. Similarly, Goodrich (1982) found that maximum snow depth and snow conditions in early winter were critical to the mean annual ground temperature regime in permafrost-affected soils. The above variables were correlated with distance to the ocean, with the thickness of vegetation and soil organic horizons and snow depth increasing and the n'-

factor and thaw depth decreasing with greater contintentality. The subsequent principal components did not extract any underlying structure of the data and are not presented here.

This research monitored temperature data over the course of only one year while more long-term records would be desirable. The mean annual temperatures for air, soil surface and in the upper soil horizon at Franklin Bluffs varied only slightly over a five-year period (Table 3.4), and the summer n'_m-factor calculated from the air and soil-surface temperatures of the stable moist nonacidic tundra varied only minimally over the same time period. Also, Shur and Slavin-Borovskiy (1993) found that the n-factor for a whole season was stable from year to year and that there was definite regularity in its geographical variation.

Thaw-depth predictions

The summer n'_m-factor information was used to predict the thaw depth of the mineral soil with a basic version of the Stefan solution. Fig. 3.7 shows the predicted versus the observed thaw-depth values. Most predicted thaw-depth values overestimated the actual values as shown in earlier studies (Romanovsky and Osterkamp, 1997). The difference between predicted and calculated values was slightly greater for the nonsorted circles than for the stable tundra, which may be explained by the fact that the Stefan solution assumes a one-dimensional homogeneous surface. However, the circles are confounded by the side effects of the surrounding well-vegetated tundra and may not thaw as deeply as predicted with the Stefan solution.

The prediction errors also varied by site. At Franklin Bluffs and Happy Valley, the predicted values were in relatively close agreement with the observed values. Farther north at Howe Island, the observed values were only 60% of the predicted values. Here, the influence of the cold ocean air may confine the thawing of the soil, leading to predictions of deeper thaw. Future studies that aim at extrapolating and predicting thaw depth of the mineral soil at the regional level could use the Stefan solution in conjunction with monitoring air temperatures and utilizing the summer n'_m-factor associated with certain vegetation types; however, without modification, the predictions might only be appropriate for the moist stable tundra of the Low Arctic in subzones D and E.

Effect of surface conditions on permafrost temperature

The vegetation canopy, soil organic horizon and snow cover act as a buffer layer between the atmosphere and the ground and thus strongly affect permafrost temperature (Luthin and Guymon, 1974). The temperature at the top of the permafrost table is the major parameter determining permafrost stability and the vulnerability of the permafrost to climate change. Here, we used the *m*ean *a*nnual mineral *s*oil-surface *t*emperature (MAST) as an approximation for permafrost temperature. The bare soils of the nonsorted circles were warmer in the summer and colder in the winter when compared to the well-vegetated adjacent tundra (Table 3.5). However, the MAST at nonsorted circles and the adjacent tundra within the same study site did not differ much, and the interactions among vegetation, snow depth and frost heave canceled out the insulative effect on the temperature regime. The MAST at Happy Valley was relatively close to the thawing

point, and the warmer soils of the bare nonsorted circles could potentially increase permafrost temperatures. However, bare nonsorted circles were small and sparsely distributed at Happy Valley, and the overall permafrost table should not be affected by the presence of nonsorted circles. When compared along the climate gradient, the mean annual air temperature differed little between the three study sites. In contrast, the MAST increased from north to south, mainly due to the insulative effect of snow at the southern end of the gradient. Here, the warming effect of snow outweighed the summer cooling effect of the vegetation, and a possible increase in winter precipitation due to climate change may lead to permafrost degradation.

Implications of climate change

Climate is expected to warm most dramatically at high latitudes in response to global atmospheric change (Houghton *et al.*, 1996; Dormann and Woodin, 2002; Chapin *et al.*, 2004; Johannessen *et al.*, 2004; Hinzman *et al.*, 2005). Climate change is likely to affect the summer and winter n'_m-factor through altered vegetation and snow properties, respectively. However, the possible effects of a changing climate on active-layer depth and permafrost are not straight forward, and two contrasting scenarios are possible: Warmer air temperatures and increased winter precipitation should drastically enhance the surface temperature of relatively bare soil, increasing the active-layer depth and possibly leading to permafrost degradation. But a warmer climate should also promote plant growth (Epstein *et al.*, 2000), thus dampening temperature extremes. The vegetation and soil organic layer would decrease the n'_m-factor and thaw depth, and could

potentially result in permafrost aggradation. Both trends might be observed along the climate gradient in northern Alaska. In subzone C and the northern parts of subzone D, warmer temperatures could promote thicker moss layers and increased plant growth especially on the nonsorted circles (Walker *et al.*, 2003), reducing the n'-factor and active-layer depth. In subzone E, the moist acidic tussock tundra might be converted to shrub tundra with greater snow and active-layer depths and eventual thawing of the upper permafrost layer in response to climate warming (Chapin *et al.*, 1995; Epstein *et al.*, 2000; Sturm *et al.*, 2001; Walker *et al.*, 2003; Sturm *et al.*, 2005).

CONCLUSIONS

In arctic tundra regions, soil disturbance through cryogenesis creates barren soil patches and arid soil phenomena within relatively humid regional climate conditions (Goryachkin *et al.*, 1999). The nonsorted circles dotting the arctic tundra have warmer summer and cooler winter temperatures, thinner vegetation mats and organic horizons, drier soils and deeper thaw depths, forming a heterogeneous, patchy landscape. The n'-factor is mostly controlled by vegetation and snow characteristics. Both the n'_v-factor and the n'_m-factor are greater for the relatively barren nonsorted circles than for the adjacent tundra with thick live vegetation, soil organic horizons and snow, and they decrease along a climate gradient from north to south. The nonsorted circles have shallower snow depths and greater overall snow densities. Thaw depth predictions based on the Stefan solution are relatively accurate in subzone D and E and overestimate the actual values in subzone C. Increased vegetation growth and snow depth associated with global climate

change might decrease the n'-factor and active-layer depth in northern tundra areas, and the morphological differences between nonsorted circles and the surrounding tundra might become less pronounced, leading to new landscape patterns.

REFERENCES

Andersland OB, and Ladanyi B. 1994. *An introduction to frozen ground engineering*. Chapman and Hall: New York.

Beringer J, Lynch AH, Chapin FS, III, Mack M, and Bonan GB. 2001. The representation of arctic soils in the land surface model: the importance of mosses. *Journal of Climate* **14**: 3324-3335.

Carlson H. 1952. Calculation of depth of thaw in frozen ground. Frost action in soils: a symposium. Highway Research Board Special Report 2, National Research Council: Washington, D.C.; 192-223.

CAVM Team. 2003. Circumpolar Arctic Vegetation Map. Scale 1:7,500,000. Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service: Anchorage.

Chapin FS, III, Peterson G, Berkes F, Callaghan TV, Angelstam P, Apps M, Beier C, Bergeron Y, Crépin A-S, Danell K, Elmqvist T, Folke C, Forbes B, Fresco N, Juday G, Niemelä J, Shvidenko A, and Whiteman G. 2004. Resilience and vulnerability of northern regions to social and environmental change. *Ambio* **33**: 344-349.

Chapin FS, III, Shaver GR, Giblin AE, Nadelhoffer KG, and Laundre JA. 1995. Response of arctic tundra to experimental and observed changes in climate. *Ecology* **76**: 694-711.

Dormann CF, and Woodin SJ. 2002. Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. *Functional Ecology* **16**: 4-18.

Epstein HE, Walker MD, Chapin FS, III, and Starfield AM. 2000. A transient, nutrient-based model of arctic plant community response to climate warming. *Ecological Applications* **10**: 824-841.

Goodrich LE. 1982. The influence of snow cover on the ground thermal regime. *Canadian Geotechnical Journal* **19**: 421-432.

Goryachkin SV, Karavaeva NA, Targulian VO, and Glazov MV. 1999. Arctic soils: spatial distribution, zonality and transformation due to global change. *Permafrost and Periglacial Processes* **10**: 235-250.

Hildebrand EE. 1983. Thaw settlement and ground temperature model for highway design in permafrost areas. In *Proceedings of the Fourth International Conference on Permafrost*, Washington, D.C.; 492-497.

Hinzman LD, Bettez ND, Bolton WR, Chapin FS, III, Dyurgerov MB, Fastie CL, Griffith B, Hollister RD, Hope A, Huntington HP, Jensen AM, Jia GJ, Jorgenson T, Kane DL, Klein DR, Kofinas G, Lynch AH, Lloyd AH, McGuire AD, Nelson FE, Oechel WC, Osterkamp TE, Racine CH, Romanovsky VE, Stone RS, Stow DA, Sturm M, Tweedie CE, Vourlitis GL, Walker MD, Walker DA, Webber PJ, Welker JM, Winker KS, and Yoshikawa K. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change* **72**: 251-298.

Hinzman LD, Goering DJ, and Kane DL. 1998. A distributed thermal model for calculating soil temperature profiles and depth of thaw in permafrost regions. *Journal of Geophysical Research* **103**: 28,975-928,991.

Hotelling H. 1933. Analysis of a complex of statistical variables into principal components. *Journal of Educational Psychology* **24**: 417-441.

Houghton JT, Meira Filho LG, Callandar BA, Harris N, Kattenberg A, and Maskell K. 1996. *Climate change 1995: the science of climate change*. Cambridge University Press: Cambridge.

Johannessen OM, Bengtsson L, Miles MW, Kuzmina SI, Semenov VA, Alekseev GV, Nagurnyi AP, Zakharov VF, Bobylev LP, Pettersson LH, K. H, and Cattle HP. 2004. Arctic climate change: observed and modeled temperature and sea-ice variability. *Tellus* **56A**: 328-341.

Kade A, Walker DA, and Raynolds MK. 2005. Plant communities and soils in cryoturbated tundra along a bioclimate gradient in the Low Arctic, Alaska. *Phytocoenologia* **35**: in press.

Klene AE, Nelson FE, and Shiklomanov NI. 2001. The n-factor as a tool in geocryological mapping: seasonal thaw in the Kuparuk River Basin, Alaska. *Physical Geography* **22**: 449-466.

Klene AE, Nelson FE, and Shiklomanov NI. 2001. The n-factor in natural landscapes: variability of air and soil-surface temperatures, Kuparuk River Basin, Alaska, U.S.A. *Arctic, Antarctic and Alpine Research* **33**: 140-148.

Luthin JN, and Guymon GL. 1974. Soil moisture-vegetation-temperature relationships in central Alaska. *Journal of Hydrology* **23**: 233-246.

Nelson FE, Hinkel KM, Shiklomanov NI, Mueller GR, Miller LL, and Walker DA. 1998. Active-layer thickness in north central Alaska: systematic sampling, scale, and spatial autocorrelation. *Journal of Geophysical Research* **103**: 28,963-928,973.

Nelson FE, Shiklomanov NI, Mueller GR, Hinkel KM, Walker DA, and Bockheim JG. 1997. Estimating active-layer thickness over a large region: Kuparuk River Basin, Alaska, U.S.A. *Arctic and Alpine Research* **29**: 367-378.

Osterkamp TE, and Romanovsky VE. 1999. Evidence for warming and thawing of discontinuous permafrost in Alaska. *Permafrost and Periglacial Processes* **10**: 17-37.

Pavlov AV, and Moskalenko NG. 2002. The thermal regime of soils in the north of Western Siberia. *Permafrost and Periglacial Processes* **13**: 43-51.

Peterson RA, and Krantz WB. 1998. A linear stability analysis for the inception of differential frost heave. In *Proceedings of the Seventh International Conference on Permafrost*, Yellowknife, Canada; 883-889.

Peterson RA, and Krantz WB. 2003. A mechanism for differential frost heave and its implications for patterned ground formation. *Journal of Geology* **49**: 69-80.

Peterson RA, Walker DA, Romanovsky VE, Knudson JA, Raynolds MK, and Krantz WB. 2003. A differential frost heave model: cryoturbation-vegetation interactions. In *Proceedings of the Eighth International Conference on Permafrost*, Zürich, Switzerland; 885-890.

Péwé TL. 1975. Quaternary geology of Alaska. Geol. Surv. Prof. pap. 835, U.S. Government Printing Office: Washington D.C.

Ping CL, Bockheim JG, Kimble JM, Michaelson GJ, and Walker DA. 1998. Characteristics of cryogenic soils along a latitudinal transect in Arctic Alaska. *Journal of Geophysical Research* **103**: 28917-28928.

Romanovsky VE, and Osterkamp TE. 1997. Thawing of the active layer on the Coastal Plain of the Alaskan Arctic. *Permafrost and Periglacial Processes* **8**: 1-22.

SAS Institute Inc. 2004. *The SAS system for Windows V8*. SAS Institute: Cary.

Shur YL, and Slavin-Borovskiy VB. 1993. N-factor maps of Russian permafrost region. In *Proceedings of the Sixth International Conference on Permafrost*, Beijing, China; 564-568.

Smith MW, and Riseborough DW. 1996. Permafrost monitoring and detection of climate change. *Permafrost and Periglacial Processes* **7**: 301-309.

Sturm M, Holmgren J, Konig M, and Morris K. 1997. The thermal conductivity of seasonal snow. *Journal of Glaciology* **43**: 26-41.

Sturm M, Racine C, and Tape K. 2001. Increasing shrub abundance in the Arctic. *Nature* **411**: 546-547.

Sturm M, Schimel J, Michaelson G, Welker JM, Oberbauer SF, Liston GE, Fahnestock J, and Romanovsky VE. 2005. Winter biological processes could help convert arctic tundra to shrubland. *BioScience* **1**: 17-26.

Taylor AE. 2001. Relationship of ground temperatures to air temperatures in forests. In *The physical environment of the Mackenzie Valley: a baseline for the assessment of environmental change*, Dyke LD, and Brooks GR (eds). Geological Survey of Canada Bulletin: Ottawa; 111-117.

Walker DA. 2000. Hierarchical subdivision of arctic tundra based on vegetation response to climate, parent material and topography. *Global Change Biology* **6**: 19-34.

Walker DA, Epstein HE, Gould WA, Kelley AM, Kade A, Knudson JA, Krantz WB, Michaelson GJ, Peterson RA, Ping CL, Raynolds MK, Romanovsky VE, and Shur Y. 2004. Frost-boil ecosystems: complex interactions between landforms, soils, vegetation and climate. *Permafrost and Periglacial Processes* **15**: 171-188.

Walker DA, Jia GJ, Epstein HE, Raynolds MK, Chapin FS, III, Copass C, Hinzman LD, Knudson JA, Maier HA, Michaelson GJ, Nelson F, Ping CL, Romanovsky VE, and Shiklomanov N. 2003. Vegetation-soil-thaw-depth relationships along a low-arctic bioclimate gradient, Alaska: synthesis of information from the ATLAS studies. *Permafrost and Periglacial Processes* **14**: 103-123.

Washburn AL. 1980. *Geocryology: A survey of periglacial processes and environments.* John Wiley and Sons: New York.

Zhang T, Osterkamp TE, and Stamnes K. 1996. Some characteristics of the climate in northern Alaska, U.S.A. *Arctic and Alpine Research* **28**: 509-518.

Table 3.1. Summer and winter n'-factors for nonsorted circles and stable tundra plots at the three study sites. The n'-factors were recorded at the interface of live vegetation and organic matter (n'_v), and at the surface of the mineral soil (n'_m). Means are shown with standard errors in parentheses. Superscript letters indicate significant differences at α=0.01 between circles and tundra within a study site for each season and for each the n'_v- and n'_m-factor.

Study site	Summer		Winter	
	n'_v-factor	n'_m-factor	n'_v-factor	n'_m-factor
Howe Island (C)				
Bare circle	-	1.43^a (0.02)	-	0.94^a (0.01)
Tundra	-	0.99^b (0.02)	-	0.87^b (0.01)
Franklin Bluffs (D)				
Bare circle	-	0.97^a (0.03)	-	0.73^a (0.01)
Tundra	0.91 (0.01)	0.35^b (0.01)	0.57 (0.01)	0.53^b (0.02)
Happy Valley (E)				
Bare circle	-	0.74^a (0.01)	-	0.35^a (0.01)
Vegetated circle	0.89^a (0.01)	0.34^b (0.01)	0.41^a (0.01)	0.34^{ab} (0.01)
Tundra	0.76^b (0.01)	0.17^c (0.01)	0.35^b (0.01)	0.32^b (0.01)

Table 3.2. Snow profiles of representative nonsorted circles and adjacent stable tundra plots at the three study sites recorded in mid-April 2004. Snow layers are described from top to bottom.

Study site	Circle: Layer (cm)	Tundra: Layer (cm)	Grain shape	Hardness
Howe Island (C)	5-6	11-12	Surface hoar	Very low
	4-5	9-11	Loose, small rounded grains	Medium
	1-4	5-9	Wind slab	High
	0-1	0-5	Cup crystals	Very low
Franklin Bluffs (D)	16-20	25-36	Loose, small rounded grains	Low
	10-16	18-25	Wind slab	Medium
	9-10	16-18	Ice layer	High
	4-9	13-16	Loose, small rounded grains	Medium
	0-4	0-13	Columns of depth hoar	Very low
Happy Valley (E)	42-61	55-73	Loose, small rounded grains	Very low
	27-42	33-55	Wind slab	Medium
	25-27	31-32	Ice layer	High
	14-25	20-31	Loose, large rounded grains	Medium
	0-14	0-20	Columns of depth hoar	Very low

Table 3.3. The loadings (Eigenvectors) of the rescaled data of thickness of the vegetation mat and soil organic horizon, snow depth, summer and winter n'-factor at the mineral soil surface (n'_m), distance to the ocean, thaw depth of the mineral soil, snow density and soil moisture for the first principal component (PC). The variance (Eigenvalue) of the first principal component and the percent of the variation explained are shown.

Eigenvectors	**PC 1**
Thickness of vegetation and organic horizon	-0.75
Snow depth	-0.39
Summer n'_m-factor	0.34
Distance to ocean	-0.26
Thaw depth	0.22
Winter n'_m-factor	0.20
Snow density	0.11
Soil moisture	-0.08
Eigenvalue	0.04
% variance explained	79.0

Table 3.4. Mean annual temperatures for air, soil surface and soil at 0.7 m depth, and the summer n'-factor for stable moist nonacidic tundra at Franklin Bluffs. The height of temperature recording is shown in parentheses.

Year	Mean annual temperature (°C)			Summer n'-factor
	Air (2.0 m)	Soil surface (0.07 m)	Soil (-0.7 m)	
1999	-13.2	-3.6	-4.3	1.20
2000	-11.9	-5.6	-5.9	1.17
2001	-12.0	-6.1	-5.9	1.21
2002	-9.6	-3.5	-4.3	1.20
2003	-10.7	-4.6	-5.1	1.24

Table 3.5. Mean annual, July and January temperatures for the hydrological year September 2003 through August 2004 for air and the mineral soil surface at the three study sites. Mean annual temperatures at the mineral soil surface are shown for bare and vegetated nonsorted circles and adjacent tundra plots, with standard errors in parentheses.

Study sites	Mean annual temp. (°C)		Mean July temp. (°C)		Mean January temp. (°C)	
	Air	Mineral soil	Air	Mineral soil	Air	Mineral soil
Howe Island (C)	-10.9		6.2		-24.3	
Bare circle		-9.6 (0.1)		8.6 (0.1)		-23.1 (0.2)
Tundra		-9.3 (0.1)		6.6 (0.1)		-21.0 (0.2)
Franklin Bluffs (D)	-11.3		12.0		-29.1	
Bare circle		-7.5 (0.2)		11.5 (0.2)		-19.6 (0.4)
Tundra		-6.5 (0.2)		4.3 (0.3)		-13.5 (0.4)
Happy Valley (E)	-10.2		13.2		-28.0	
Bare circle		-2.3 (0.1)		9.7 (0.2)		-9.1 (0.1)
Vegetated circle		-3.4 (0.1)		5.5 (0.1)		-8.7 (0.3)
Tundra		-3.6 (0.1)		2.4 (0.1)		-7.9 (0.1)

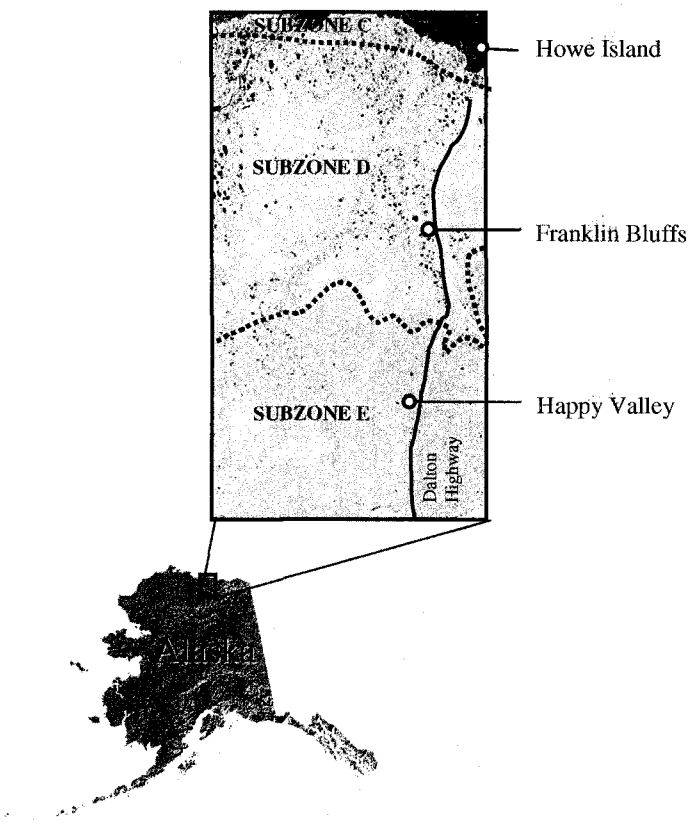

Fig. 3.1. Location of the three study sites and the respective bioclimatic subzones along the northern segment of the Dalton Highway, Alaska.

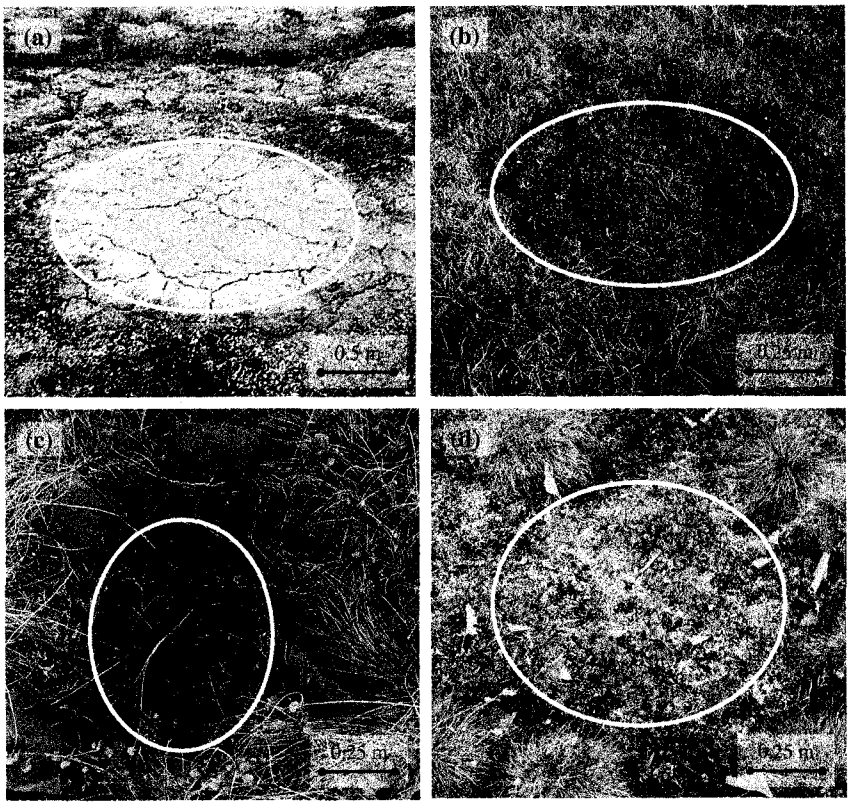

Fig. 3.2. Nonsorted circles and adjacent stable tundra at the three study sites. (a) Bare nonsorted circle at Howe Island. (b) Bare to slightly vegetated nonsorted circle at Franklin Bluffs. (c) Bare nonsorted circle at Happy Valley. (d) Vegetated nonsorted circles at Happy Valley.

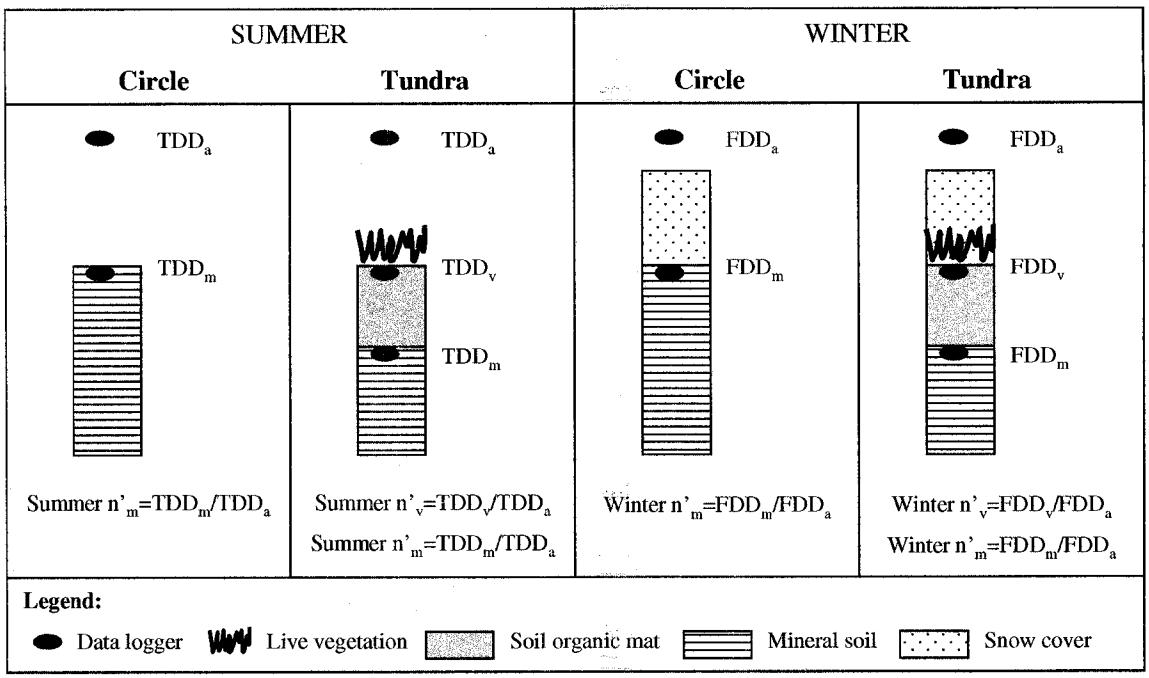

Fig. 3.3. Diagram showing the location of the temperature loggers in the nonsorted circles and the adjacent stable tundra. For each logger position, the derived thawing degree day sums for the air (TDD_a), under the live vegetation (TDD_v) and at the top of the mineral soil (TDD_m) are indicated for the summer situation, and the freezing degree day sums for the air (FDD_a), under the live vegetation (FDD_v) and at the top of the mineral soil (FDD_m) are indicated for the winter situation. Calculations for the n'-factor as an index of thermal insulation under the live vegetation (n'_v) and at the mineral soil surface (n'_m) are shown.

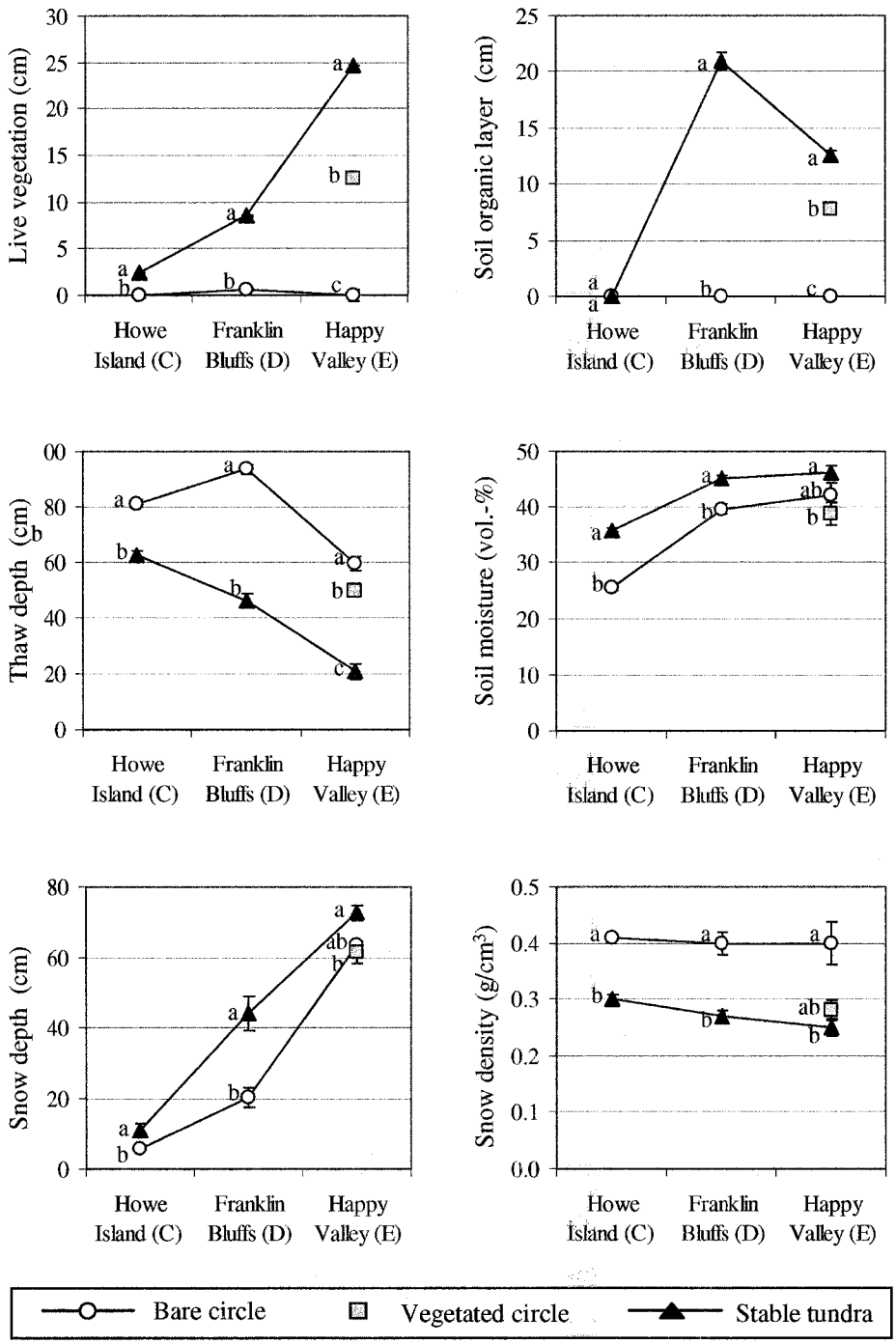

Fig. 3.4. The thickness of the live vegetation and soil organic layer, thaw depth and soil moisture of the mineral soil, snow depth and snow density for bare and vegetated nonsorted circles and adjacent stable tundra at the three study sites. Letters indicate significant differences at α=0.05 between circles and tundra within a study site. Means with standard errors are shown.

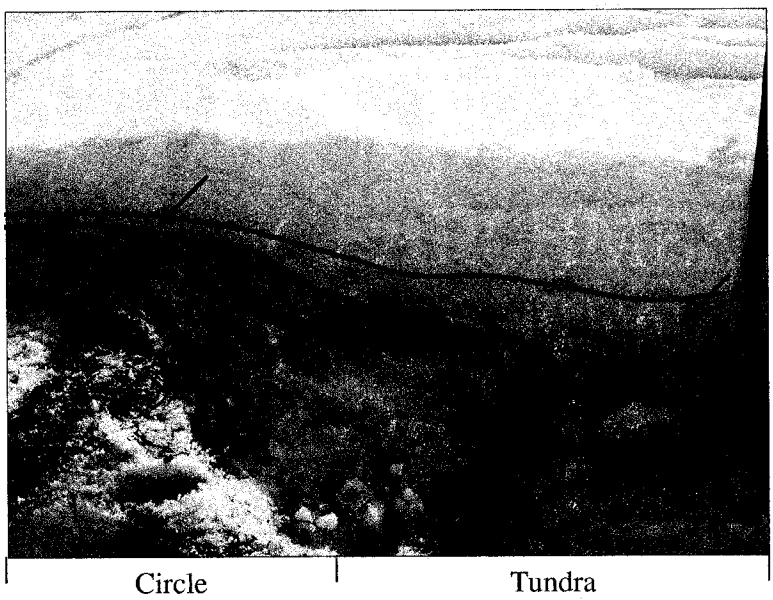

Fig. 3.5. Snow profile across a nonsorted circle and the adjacent tundra. The arrows indicate the depth-hoar layer.

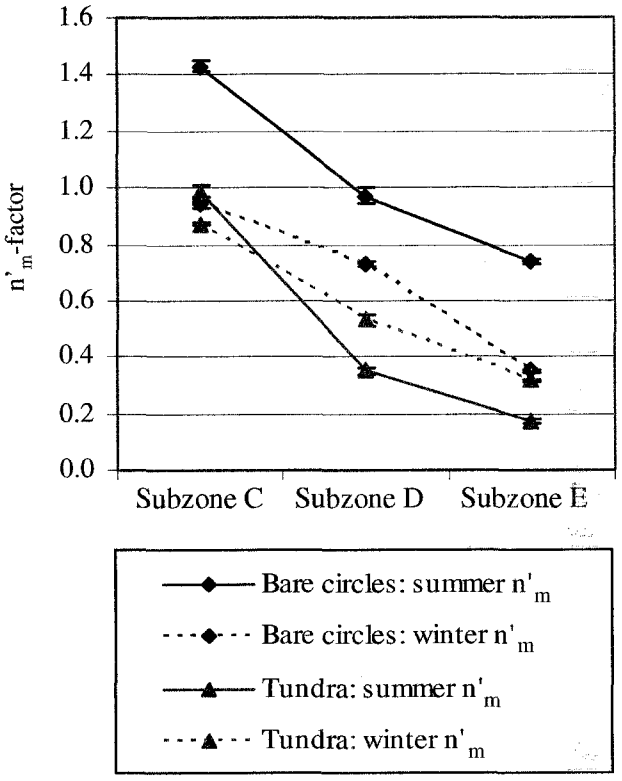

Fig. 3.6. Summer and winter n'-factors at the mineral soil surface (n'_m) for bare nonsorted circles and stable tundra plots. Means with standard errors are shown along the bioclimate gradient from north to south.

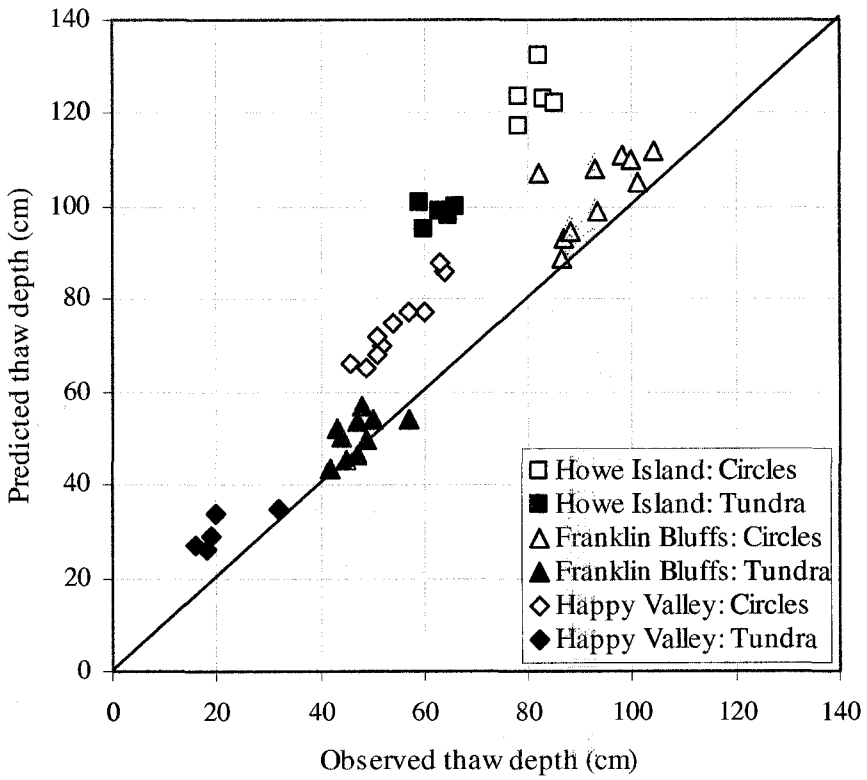

Fig. 3.7. Predicted vs. observed thaw-depth values of the mineral soil at the three study sites. Each study site has a set of relatively shallow thaw values (stable tundra) and a set of relatively deep values (nonsorted circles).

CHAPTER 4: EXPERIMENTAL ALTERATION OF VEGETATION ON NONSORTED CIRCLES: EFFECTS ON CRYOGENIC PROCESSES AND IMPLICATIONS FOR CLIMATE CHANGE IN THE ARCTIC

[*] Submitted as: Kade A, and Walker DA. 2006. Experimental alteration of vegetation on nonsorted circles: effects on cryogenic processes and implications for climate change in the Arctic. *Global Change Biology* (submitted).

ABSTRACT

Nonsorted circles, patterned-ground features caused by differential frost heave, are a common component of landscapes in most Low Arctic tundra regions. Climate change will likely affect the structure of arctic vegetation. We were interested in how changes to the vegetation might affect patterned-ground features and the associated cryogenic processes. We selected 28 nonsorted circles similar in size and vegetation characteristics at a moist nonacidic tundra site in northern Alaska. An area of 0.5 m^2 was marked in the center of each circle and received one of four treatments (n = 7): (a) vegetation removal; (b) vegetation removal and sedge transplants; (c) vegetation removal and moss transplants; or (d) no manipulation. We monitored soil-surface temperatures, thaw depth, frost heave and soil-surface instability as indicators of cryogenic processes for three years.

Vegetation removal led to greater summer temperatures at the soil surface, increasing mean thaw depth by 4.8 ± 0.5 cm and frost heave by 3.3 ± 0.5 cm when compared to the means of the control (77.6 ± 0.6 cm and 12.6 ± 0.6 cm, respectively), and increasing annual soil-surface instability. In contrast, moss additions lowered soil temperatures in the summer and delayed freezing and thawing. The moss treatments decreased mean thaw depth by 10.6 ± 0.6 cm and frost heave by 6.6 ± 0.4 cm when compared to the control, and reduced soil-surface instability. In the sedge plots, the effects on thaw and heave were intermediate to the vegetation-removal and moss-addition treatments, as were the control plots. The sedge transplants did not expand their root systems until the third year due to frost heaving and needle-ice formation.

This study suggests that a possible biomass increase and shift in species composition due to global climate change could decrease the heat flux between the atmosphere and soil, thaw depth and frost heave, and potentially result in the loss of nonsorted circles. This may lead to lower species diversity and landscape heterogeneity, greater soil moisture, slower decomposition, less soil nutrients and greater carbon sequestration.

INTRODUCTION

The vegetation and soil patterns in many permafrost regions are influenced by the distribution of nonsorted circles (Fig. 4.1), which are relatively bare, patterned-ground features measuring 0.5 to 3 m across. Other terms for nonsorted circles include frost scars (Sigafoos, 1951; Johnson and Neiland, 1983), frost boils (Gartner *et al.*, 1986; Chernov and Matveyeva, 1997; Walker *et al.*, 2004), mud boils (Zoltai and Tarnocai, 1981) and spot medallions (Popov *et al.*, 1963). Nonsorted circles are caused by *differential frost heave* that occurs when ice lenses form in soils during winter. The soils within the nonsorted circles heave more than in the surrounding tundra due to a deeper active layer where more ice lenses can form (Peterson and Krantz, 2003). In addition, free-moving water with high free energy migrates from the surrounding tundra soils to the freezing front of the nonsorted circles due to cryostatic suction (Williams and Smith, 1989), resulting in differentially greater frost heave. Differential frost heave and needle-ice formation control the formation and maintenance of the nonsorted circles (Peterson and Krantz, 1998; Walker *et al.*, 2004). *Needle ice* consists of elongated ice crystals that grow

just beneath the soil surface when steep diurnal temperature gradients exist (Hallet, 1990), often pushing the surface layer upwards. Strong soil-surface disturbance due to needle-ice formation and frost cracking has a negative impact on plant roots and results in little vegetation cover and shallow organic horizons in the centers of the active circles. In turn, the sparse plant canopy provides only minimal insulation at the soil surface, which results in deeper thaw depths in late summer and more heave during the winter.

The interactions among the components of the cryoturbated tundra are strongly controlled by the regional climate, and nonsorted circles should be highly susceptible to environmental change as they seem to be abundant only under certain environmental conditions (Walker *et al.*, 2004). Climate is expected to warm most dramatically at high latitudes in response to global atmospheric change (Intergovernmental Panel on Climate Change (IPCC), 2001; Dormann and Woodin, 2002; Johannessen *et al.*, 2004; Hinzman *et al.*, 2005) and could have major impacts on vegetation patterns, permafrost degradation and nutrient cycling (Chapin *et al.*, 2004; Hinzman *et al.*, 2005; Sturm *et al.*, 2005). Shifts in species composition and increased vegetation growth (Chapin *et al.*, 1995; Epstein *et al.*, 2000) could also alter the cryogenic processes within nonsorted circles and lead to new landscape patterns. This could change a wide variety of ecosystem properties that are affected by the presence of nonsorted circles, including species diversity, plant biomass, decomposition rates, soil moisture and nutrient status, carbon sequestration, and heat and trace gas fluxes (Walker *et al.*, 1998; Walker *et al.*, 2004).

Several studies have investigated the effect of patterned ground on plant distributions (e.g. Sigafoos, 1951; Johnson and Neiland, 1983; Jonasson and Sköld, 1983;

Gartner *et al.*, 1986; e.g. Anderson and Bliss, 1998; Cannone *et al.*, 2004; Walker *et al.*, 2004) and the influence of tundra vegetation on soil temperatures and thaw depth (Price, 1971; Beringer *et al.*, 2001; Klene *et al.*, 2001; Pavlov and Moskalenko, 2002). However, no study to date has focused on the effect of vegetation on the thermal properties and cryogenic processes associated with patterned-ground features. Here, we investigate following question: How does vegetation affect the thermal regime, thaw depth, frost heave and soil-surface stability within nonsorted circles? We manipulated the vegetation canopy on nonsorted circles and monitored soil-surface temperatures, thaw depth, frost heave, snow depth and soil-surface stability as indicators of cryogenic processes over the course of three years. We examined how these variables are affected by (a) the absence of vegetation, (b) vascular plants with an extensive, soil-stabilizing root system, or (c) a thick, insulating moss carpet.

MATERIALS AND METHODS

Study area

We conducted the experiment in the Sagwon Hills near the Dalton Highway in Northern Alaska (Fig. 4.2, 69°25'58" N, 148°40'23" W, elevation 280 m). The study site is situated at the northern end of the Arctic Foothills, where broad rounded hills with elevations up to 350 m dominate the landscape. In the Arctic Foothills region, mean annual air temperatures range from -7 to -10 °C, and mean annual precipitation ranges from 140-270 mm, 40% of which falls as snow (Haugen, 1982). The site has a thin loess mantle over Tertiary outwash gravel. The soils have developed on fine-textured

materials, mainly silt loams, and are calcareous (Bockheim *et al.*, 1998). The soils contain permafrost within 1 m of the soil surface and show strong signs of soil mixing due to cryoturbation (Ping *et al.*, 1998). According to the Circumpolar Arctic Vegetation Map (CAVM Team, 2003), the field site is within bioclimate subzone D. The zonal vegetation is non-tussock-sedge, dwarf-shrub, moss tundra consisting of the association Dryado integrifoliae-Caricetum bigelowii (Walker *et al.*, 1994; Kade *et al.*, 2005).

Nonsorted circles are common and cover approximately 35% of the landscape. They measure about 1 m in diameter and are sparsely vegetated. The thin vegetation mat on the nonsorted circles belongs to the association Junco biglumis-Dryadetum integrifoliae (Kade *et al.*, 2005) and consists mainly of the dwarf shrub *Dryas integrifolia* and several lichen species. Small bare areas are exposed as a result of active soil churning. The adjacent tundra is well vegetated and dominated by *Dryas integrifolia*, several willow and sedge species and thick moss mats consisting mainly of *Hylocomnium splendens* and *Tomentypnum nitens* (Association Dryado integrifoliae-Caricetum bigelowii Walker *et al.*, 1994).

Experimental setup

We selected 28 nonsorted circles with similar environmental characteristics as study plots and marked an area of 0.5 m^2 in the center of each plot for manipulation. In July 2002, four groups of seven nonsorted circles were randomly selected to receive one of the following treatments (Fig. 4.3): (a) Vegetation removal: We cleared the existing vegetation mat from the nonsorted circles with a knife, and the underlying mineral soil

was exposed. (b) Vegetation removal and sedge transplants: We collected small *Eriophorum vaginatum* tussocks from the surrounding tundra, which we transplanted at 10 cm intervals into the nonsorted circles after the vegetation was removed. Each plot received a total of 49 small tussocks, which were about 10 cm tall. (c) Vegetation removal and moss-carpet transplants: We cut moss slabs consisting mainly of the pleurocarpous species *Hylocomium splendens* and *Tomentypnum nitens* of about 15 cm thickness from the surrounding tundra and placed them on the nonsorted circles once the vegetation was removed. (d) Control: The plots were not manipulated. Each summer, we weeded the bare and sedge plots to maintain the treatment.

At each plot, the soil temperature at 1 cm depth was recorded hourly during September 2002 through August 2005 with a Hobo H8 data logger (Onset Computer Corporation, 2000). We measured maximum thaw depth in early September 2003-2005 by pushing a 1 cm-diameter rod through the active layer. We pounded 1.5 cm-diameter rebar at least 80 cm into the permafrost at the center of each study plot and measured the distance from the top of the bar to the ground surface in the summer and at the end of the winter. The heave was calculated as the difference between the summer and winter measurements. We recorded maximum frost heave and maximum snow depth in mid April 2003-2005. We determined soil-surface instability due to needle-ice formation with the help of a "toothpick index" (Gartner *et al.*, 1986). In July 2002, each plot received 25 evenly distributed toothpicks or shish kebab sticks depending on the physiognomy of the plant cover. Toothpicks were inserted upright half their length (3 cm) into the ground in the control, bare and sedge plots. The moss treatments received 25 30 cm-long shish

kebab sticks per plot, as it was impossible to locate the toothpicks under the moss mat. Although not directly comparable, we inserted the shish kebab sticks to the same depth as the toothpicks (3 cm). After one year, we recorded the number of straight, visibly tilted or expelled toothpicks and shish kebab sticks (here referred to jointly as picks). Picks that were moved upwards due to frost action and expelled from the soil but still supported by the surrounding vegetation were reported as expelled. We transformed the data into an index of soil-surface instability. We multiplied the number of straight picks by 0, tilted picks by 1 and expelled picks by 2, and summed up the scores for each plot, with the maximum possible soil-surface instability being a total score of 50. We repeated the pick measurements over the course of three years.

Data were analyzed using SAS (SAS Institute Inc., 2004). We performed repeated measure analyses for each response variable (soil temperature, thaw depth, frost heave, snow depth, soil-surface stability) to determine whether the four treatment groups had simultaneously similar response patterns over time. The results for an effect of time were non-significant for most response variables, and we report the data of the last experimental year. We used univariate one-way analyses of variance with Tukey's W procedure (α=0.05) to estimate treatment differences (Tukey, 1953).

RESULTS

Soil temperatures

The overall pattern of the daily mean soil temperatures at 1 cm depth for the control plots over the course of three years is shown in Fig. 4.4a. Temperatures ranged

from 15 °C in the summer to -25 °C in the winter. The differences in soil temperatures between the three vegetation manipulations and the control are illustrated in Fig. 4.4b. Soil temperatures varied greatly among treatments in the summer. The bare and sedge plots were up to 4 °C warmer than the control, and the moss treatments up to 8 °C cooler. The vegetation-removal treatments increased the mean summer soil temperatures (June through August) by 1.5 °C when compared to the control, and the moss-addition treatments decreased the mean summer soil temperatures by 2.8 °C (Table 4.1). The sedge plots had a relatively large portion of bare soil, and the mean summer soil temperatures were only slightly less than for the bare plots. In the summer, the vegetation-removal and sedge treatments also had greater daily soil temperature fluctuations when compared to the control, whereas the moss-addition treatments showed very little daily fluctuation (e.g., Fig. 4.5a). As an example, from 04:00 to 15:00 on 18 July 2004, the hourly mean soil temperature at the bare plots increased 11 °C, from 10 °C to 21 °C, while the soil temperature at the moss plots increased 2 °C, from 8 °C to 10 °C. The insulation provided by the moss carpet also resulted in delayed fall freezing with soil temperatures below 0 °C and delayed spring thawing with soil temperatures above 0 °C when compared to the other treatments. In general, thawing occurred almost two weeks later and freezing one week later (Table 4.2).

During the winter months, the differences between the daily mean near-surface soil temperatures among the treatments were more compressed than in the summer months (Fig. 4.4b) due to the relatively uniform insulation of the snow cover (see discussion below). The bare plots were generally slightly cooler than the control, and the

moss plots were consistently warmer (Fig. 4.4b). The differences among the treatments were minimal during the winter 2003/04, when the overall snow depth was uncharacteristically deep. The mean winter soil temperatures (December through February) were lowest at the bare plots (mean=-18.7 °C, Table 4.1) and greatest at the moss plots (mean=-16.5 °C). The hourly temperature fluctuations were negligible for all treatments (Fig. 4.5b). For example, on 2 February 2004, the hourly mean soil temperature at 1 cm depth on the barren plots was –20.6 °C at 08:00 and –19.8 °C at 23:00, a difference of less than 1 °C. Similarly, the hourly mean soil temperature increased from –18.7 °C to –18.2 °C over the same time frame at the moss plots.

Although the vegetation had a large effect on the soil-surface temperatures in the summer and winter, the net effect on the mean annual temperatures was negligible. The mean annual soil temperatures did not differ significantly among the treatments, ranging from -6.2 °C to -6.7 °C (Table 4.1). On the vegetated plots, the cooler soil temperatures in the summer were offset by the warmer soil temperatures in the winter. The temperature differences among the treatments were greater in the summer than in the winter, indicating that the winter conditions were more important in determining the overall annual temperatures, thus overriding the summer differences.

Thaw depth

The bare plots had the greatest thaw depths (mean 82.4 cm, Table 4.1), and the sedge and control plots had slightly shallower thaw depths (means 77.0 and 77.6 cm, respectively). The thaw depth was least at the moss plots (mean 66.0 cm). When

compared to the control, the bare plots showed an increase in thaw depth by 6%, and the moss-addition treatments decreased the thaw depth by 15%.

Frost heave

The frost heave of the control plots averaged 12.6 cm (Table 4.1). The bare plots heaved about 3.3 cm more than the control plots, while the sedge plots experienced heave similar to the control plots. The moss-addition treatments heaved about 6.6 cm less than the control plots. The bare plots increased frost heave by 26% when compared to the control, and the moss plots decreased frost heave by 52%.

Snow depth

The snow measurements reflected the effect of the vegetation treatments on the relative elevation of the plot surface. The bare plots had a lower surface after the removal of the vegetation, and the sedge and moss treatments had relatively higher surfaces with the addition of the transplants. In the winter, the snow formed a relatively level cover across the landscape that masked the variations in micro-topography. The bare plots therefore had the deepest snow depths (mean 25.9 cm, Table 4.1), while the moss plots had the thinnest snow cover (mean 15.7 cm). The sedge and control plots had intermediate snow depths.

Soil-surface instability

The instability of the soil surface was reflected in the toothpick index, where a high value corresponded to a large number of tilted or expelled picks. This index does not indicate quantitative differences in stability because an expelled pick does not indicate twice the cryoturbation amount of a tilted pick. The soils of the control and moss plots were very stable; whereas, the bare plots had the greatest soil-surface instability, with most toothpicks being expelled from the soil after one year (Table 4.1). The soil-surface stability of the sedge plots increased over the course of the experiment (index of soil instability: 42 in 2003, 40 in 2004, and 25 in 2005). After the first year, most sedge transplants did not expand their rooting system and were heaved about 3 cm out of the ground. We pushed the sedge transplants back into the soil each summer; and at the end of the experiment, all transplants put out fibrous roots into the surrounding soil, leading to more stable soils.

DISCUSSION

Interactions among system components

The different plant functional types and their insulation properties have a significant impact on the cryogenic regime of the nonsorted circles. The interactions among the major variables affecting the cryogenic regime of the manipulated study plots are shown in a conceptual model (Fig. 4.6). The vegetation canopy has a direct effect on soil temperatures, especially in the summer. Thick moss carpets buffer the thermal regime at the soil surface, leading to small diurnal temperature amplitudes, low summer

temperatures and delayed freezing and thawing dates. This agrees with Pavlov and Moskalenko (2002), who monitored the thermal regime of tundra soils on the Yamal Peninsula in Western Siberia. They estimated that the mean annual cooling effect of a 5-cm thick vegetation and litter layer is 0.5-1.5 °C on soil temperatures, delaying soil thawing in the summer. Beringer *et al.* (2001) modeled soil temperatures at 0.5 m depth of various tundra soils for northern Alaska. Their results show that a 25-cm thick moss and peat layer insulates the underlying soil, lowering soil temperatures by 6.9 °C in the summer when compared to a homogenous loam soil column.

Several previous studies have reported the linkage between vegetation and thaw depth (Price, 1971; Anderson and Bliss, 1998; Nelson *et al.*, 1998; Beringer *et al.*, 2001; Klene *et al.*, 2001; Pavlov and Moskalenko, 2002; Walker *et al.*, 2003; Kade *et al.*, 2005). The effects of vegetation removal and moss addition on thaw depth and frost heave in this experiment are illustrated in Fig. 4.7. The sedge treatments showed responses similar to the lightly vegetated control plots and are not mentioned separately. The thaw depth was closely linked to the soil-surface temperatures during the summer months, and the warm bare plots had the greatest thaw depths. In contrast, the moss carpets delayed the onset of thawing, shaded the underlying mineral soil, and prevented it from warming during the summer, resulting in shallower thaw depths (Fig. 4.7).

Frost heave is caused by ice-lens formation during the winter and the resulting increase in the soil volume. Our vegetation-removal plots heaved 3.3 cm (26%) more than the control plots (Fig. 4.7), which can partly be explained by the deeper thaw depth allowing for more ice lenses to form. The moss treatments reduced mean frost heave by

6.6 cm (52%) when compared to the control, presumably as a result of decreased thaw depth and delayed freeze-up (Table 4.2) and thus reduced ice-lens formation. The depth of the active layer directly affected the amount of frost heave of the nonsorted circles. In both treatments, the percentage change in frost heave was about three to four times the percentage change in the thaw depth. If the heave was due to only the water in the soil column of the nonsorted circle, the percentage change of heave should be the same as the percentage change in the thaw depth when compared to the control. The excess water for ice-lens formation had to come from the adjacent tundra areas, possibly either through the slow movement of ground water or through cryostatic suction.

The vegetation had a major impact on soil-surface instability. The soils of the control and moss plots were relatively stable, whereas the bare plots had the greatest soil-surface instability. This agrees with Gartner *et al.* (1986), who reported greater surface stability as indicated by toothpick movement in vegetated tundra micro-habitats of lichen and moss mats than in unvegetated nonsorted circles. At the bare study plots, the soils were disturbed by frost heave and needle-ice formation. Although we did not study needle ice (or pipkrakes) *per se*, we noticed that the soils of the bare plots and the bare portions of the sedge and control plots had a loose and crumbly "cottage cheese" structure as the result of needle-ice formation. Needle-ice crystals form during the early summer and fall, when steep temperature gradients exist between the air and soil (Washburn, 1980). Where the vegetation is absent, the needle ice pushes the soil-surface layer upwards and decreases soil-surface stability. The plants can also stabilize the soil with their root system, as indicated in the sedge treatment. The fibrous root mats help

keep the soil surface more stable. In this experiment, it took three years for the sedge seedlings to develop sufficient root systems to keep them from being heaved out of the soil. The soil heaving was probably the main factor preventing *Eriophorum vaginatum* from colonizing bare nonsorted circles. It may also explain why this sedge species is often found in rings around nonsorted circles. *Eriophorum vaginatum* requires mineral soils to establish, so it may find the margins of the barren patches sufficiently stable without getting into the highly competitive peaty environment of the inter-circle areas. The instability of the bare soil surfaces of nonsorted circles is likely to reduce plant establishment (Johnson and Neiland, 1983; Anderson and Bliss, 1998) and delay successional trends (Sigafoos, 1951; Haugland and Beatty, 2005). However, the soil disturbance may also be important in providing the main opportunity for seedling regeneration (Gartner *et al.*, 1986; Gough, 2006). The negative impact of unstable soils on plant roots and succession allows only thin vegetation mats composed mostly of lichens, small mosses and small vascular plants that can establish in small crevices of the barren surfaces and withstand repeated soil movement (e.g. *Braya purpurascens*, *Chrysanthemum integrifolium*, *Dryas integrifolia*, *Juncus biglumis*, *Saxifraga oppositifolia*, *Toffieldia coccinea*).

The insulation caused by snow probably did not affect the cryogenic regime in this experiment because the winter temperatures were relatively similar among treatments. Also, frost heaving should already be at its maximum in early winter and not be strongly influenced by soil temperatures throughout the winter. Soil moisture, which is thought to be an important factor in the development of nonsorted circles (Peterson and

Krantz, 2003), was not measured continuously in this experiment. However, as the study was only conducted at one site, soil moisture at deeper depth probably did not differ much among treatment plots and would have had no major influence on cryogenic processes. It would be useful to repeat this type of experiment at several localities with different site variables and then compare the influence of soil moisture, soil texture and local climate on the cryogenic regime.

Implications for climate change

Vegetation patterns

Climate change in arctic ecosystems is expected to have major effects on vegetation patterns, nutrient cycling and the permafrost table (Osterkamp and Romanovsky, 1999; Chapin *et al.*, 2004; Hinzman *et al.*, 2005). A warming arctic climate will likely result in increased biomass and changes to species composition. The effect of climate warming on nonsorted-circle formation and morphology will likely vary depending on the current climate conditions and would be different in the High and Low Arctic.

In the High Arctic (areas north of the 7 °C mean July temperature isotherm), the nonsorted circles are relatively barren and the adjacent stable tundra has very little moss cover, resulting in little contrast in the thermal properties between the circle and inter-circle areas. Nonsorted circles are uncommon in the High Arctic, and most landscapes are instead dominated by small nonsorted polygons, the result of little frost cracking or desiccation. Warmer temperatures in the High Arctic might favor the development of

greater plant cover and thicker moss carpets in more stable areas between the nonsorted polygons, resulting in a greater contrast in soil thermal properties between the polygons and adjacent tundra with greater differential frost heave (the difference in heave between the circles and stable tundra) and potentially leading to the development of nonsorted circles. The nonsorted circles themselves would likely remain barren due to strong frost heave and needle-ice development (Walker *et al.*, 2003). Nonsorted circles and polygons in the High Arctic have also been shown to have high salt concentrations in the surface soils because of high evapotranspiration rates (Kade *et al.*, 2005; Michaelson *et al.*, 2005), further hindering plant establishment and growth.

In the Low Arctic, the potential effects of climate warming will depend on the type of tundra vegetation. Two distinctly different vegetation types cover large areas of the Arctic in Alaska. Moist nonacidic tundra generally occurs on stable zonal sites with surface soil pH greater than 5.5, and moist acidic tundra occurs on zonal sites with soil pH less than 5.5. Moist nonacidic tundra is dominated by prostrate dwarf shrubs, grasses and lichens, and has lower phytomass, thinner soil organic horizons, greater ground heat flux and deeper active layers than the moist acidic tundra (Walker *et al.*, 1998; Walker *et al.*, 2001; Eugster *et al.*, 2005). The nonacidic tundra also shows more bare soil due to the abundance of large, relatively active nonsorted circles. There are also noticeable differences in the character of the vegetation growing on the nonsorted circles as one travels south from the coast in northern Alaska (Kade *et al.*, 2005). There is a general increase in both the horizontal density of vegetation and the thickness of the plant canopy growing on the nonsorted circles. Mosses in particular are more abundant. Thus, in

nonacidic areas, climate warming would likely favor moss growth in both circle and inter-circle areas (Walker *et al.*, 2003), resulting in the cooling of the nonsorted circles and masking the morphological differences between circles and stable tundra.

Moist acidic tundra is dominated by erect dwarf shrubs, sedge tussocks and thick moss carpets, and the sparsely distributed nonsorted circles are well vegetated and show low cryogenic activity (Kade *et al.*, 2005). In some areas, a warming climate may lead to increased shrub abundance and could convert this moss-rich tundra type into shrub tundra with greater overall thaw depths (Chapin *et al.*, 1995; Epstein *et al.*, 2000; Sturm *et al.*, 2005), which should decrease the differential frost heave of nonsorted circles and could result in the local disappearance of these patterned-ground features.

Furthermore, changes to the nonsorted-circle system as a result of climate warming would likely affect local and landscape-level patterns of plant diversity. Nonsorted circles provide islands of habitat for certain plant communities (Kade *et al.*, 2005), increasing the alpha and beta diversity of these areas compared to landscapes without nonsorted circles. In some parts of the Low Arctic, especially warmer areas where moist nonacidic tundra occurs on loess soils, the loss of nonsorted circles could lead to a decrease in landscape heterogeneity and biodiversity.

Active layer and carbon budgets

The change in thaw depth associated with different plant canopy types could result in the release or sequestration of the organic carbon (OC) in the mineral soil (Fig. 4.7). Most studies to date predict that warmer temperatures will cause generally deeper

active layers in the Arctic, resulting in drier landscapes and increased release of trace gases to the atmosphere (Intergovernmental Panel on Climate Change, 2001). Vegetation could, however, lead to very different active-layer responses in different parts of the Arctic with important consequences on carbon budgets. Ping *et al.* (2002) reported a total OC content of 29 kg m^{-2} for the active layer of the nonacidic nonsorted circles in the Sagwon Hills, Alaska. Based on the mean thaw depth of 77.6 cm at the control plots, an increase of 4.8 cm in thaw depth as seen in the bare treatments would translate roughly to an extra 0.37 kg m^{-2} OC that is potentially decomposable. Of this amount, about 0.5% should be released first in the form of dissolved OC as part of the melt water, and the remaining 99.5% would be subject to microbial decomposition (Michaelson *et al.*, 1998). In contrast, the moss treatments decreased the mean thaw depth by 10.6 cm, which would equate to the potential sequestration in the permafrost of a total of 3.96 kg m^{-2} OC.

In the High Arctic, the potential establishment of a thin moss carpet in the inter-circle areas due to a warming climate could decrease ground heat flux and thaw depth. The effects on the carbon budget in the soil, which has very little organic carbon, would, however, be minimal. In the Low Arctic, a warmer climate could result in thicker moss carpets both on and off the nonsorted circles of the nonacidic tundra, decreasing the ground heat flux and thaw depth and sequestering carbon in an aggrading permafrost table. In other parts of the Low Arctic where shrubs could invade areas presently occupied by tussock tundra, the moss-rich acidic tundra may be converted into shrub tundra with a deeper active layer, releasing carbon to the atmosphere.

Permafrost table

The vegetation canopy and snow cover act as a buffer layer between the atmosphere and the ground, strongly affecting soil-surface and permafrost temperatures (Luthin and Guymon, 1974). This experiment found that altering the vegetation cover had large effects on the summer soil-surface temperatures, but had no significant effect on the *annual* mean soil temperatures at the top of the mineral soil. Although we did not measure the temperatures at the top of the permafrost table, this result suggests that permafrost temperatures were not affected locally by the experimental manipulations. Interestingly, it implies that although vegetation changes can have major effects on active layers, they may have relatively little effect on local permafrost temperatures.

CONCLUSIONS

The different plant canopy types and their insulation properties play a major role within the patterned-ground system, mainly by influencing near-surface soil temperatures. Thick vegetation mats act as an insulative layer producing cooler summer temperatures and delaying thawing and freezing of the soil. Shallower active layers and delayed freezing result in decreased ice-lens formation and frost heave. In contrast, bare soils allow for deeper thaw depths in the summer and presumably the formation of more ice lenses and thus greater frost heave in winter. The bare soils also experience less soil-surface stability due to frost heaving and the formation of needle ice. This in turn should prevent plant succession and the formation of a continuous vegetation mat, reinforcing cryogenic processes. Increased moss production and/or shifts of vegetation zones as a

result of a warming arctic climate should decrease the cryogenic activity of nonsorted circles in the Low Arctic. The potential local disappearance of nonsorted circles, particularly in the moist nonacidic tundra of the Low Arctic, could result in decreased landscape heterogeneity and greater carbon sequestration in the aggrading permafrost table.

REFERENCES

Anderson DG, and Bliss LC. 1998. Association of plant distribution patterns and microenvironments on patterned ground in a polar desert, Devon Island, N.W.T., Canada. *Arctic and Alpine Research* **30**: 97-107.

Beringer J, Lynch AH, Chapin FS, III, Mack M, and Bonan GB. 2001. The representation of arctic soils in the land surface model: the importance of mosses. *Journal of Climate* **14**: 3324-3335.

Bockheim JG, Walker DA, and Everett KR. 1998. Soil carbon distribution in nonacidic and acidic tundra of arctic Alaska. In *Soil processes and the carbon cycle*, Lal R, Kimble JM, Follett RF, and Stewart BA (eds). CRC Press: New York.

Cannone N, Guglielmin M, and Gerdol R. 2004. Relationships between vegetation patterns and periglacial landforms in northwestern Svalbard. *Polar Biology* **27**: 562-571.

CAVM Team. 2003. Circumpolar Arctic Vegetation Map. Scale 1:7,500,000. Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service: Anchorage.

Chapin FS, III, Peterson G, Berkes F, Callaghan TV, Angelstam P, Apps M, Beier C, Bergeron Y, Crépin A-S, Danell K, Elmqvist T, Folke C, Forbes B, Fresco N, Juday G, Niemelä J, Shvidenko A, and Whiteman G. 2004. Resilience and vulnerability of northern regions to social and environmental change. *Ambio* **33**: 344-349.

Chapin FS, III, Shaver GR, Giblin AE, Nadelhoffer KG, and Laundre JA. 1995. Response of arctic tundra to experimental and observed changes in climate. *Ecology* **76**: 694-711.

Chernov YI, and Matveyeva NV. 1997. Arctic ecosystems in Russia. In *Ecosystems of the world, vol. 3: Polar and alpine tundra*, Wielgolaski FE (ed). Elsevier: Amsterdam; 361-507.

Dormann CF, and Woodin SJ. 2002. Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. *Functional Ecology* **16**: 4-18.

Epstein HE, Walker MD, Chapin FS, III, and Starfield AM. 2000. A transient, nutrient-based model of arctic plant community response to climate warming. *Ecological Applications* **10**: 824-841.

Eugster W, McFadden JP, and Chapin FS, III. 2005. Differences in surface roughness, energy, and CO_2 fluxes in two moist tundra vegetation types, Kuparuk watershed, Alaska, U.S.A. *Arctic, Antarctic and Alpine Research* **37**: 61-67.

Gartner BL, Chapin FS, III, and Shaver GR. 1986. Reproduction of *Eriophorum vaginatum* by seed in Alaskan tussock tundra. *Journal of Ecology* **74**: 1-18.

Gough L. 2006. Neighbor effects on germination, survival, and growth in two arctic tundra plant communities. *Ecography* **29**: 1-13.

Hallet B. 1990. Self-organization in freezing soils: from microscopic ice lenses to patterned ground. *Canadian Journal of Physics* **68**: 842-852.

Haugen RK. 1982. Climate of remote areas in north-central Alaska: 1975-1979 summary. U.S. Army Cold Regions Research and Engineering Laboratory: Hanover, New Hampshire.

Haugland JE, and Beatty SW. 2005. Vegetation establishment, succession and microsite frost disturbance on glacier forelands within patterned ground chronosequences. *Journal of Biogeography* **32**: 145-153.

Hinzman LD, Bettez ND, Bolton WR, Chapin FS, III, Dyurgerov MB, Fastie CL, Griffith B, Hollister RD, Hope A, Huntington HP, Jensen AM, Jia GJ, Jorgenson T, Kane DL, Klein DR, Kofinas G, Lynch AH, Lloyd AH, McGuire AD, Nelson FE, Oechel WC, Osterkamp TE, Racine CH, Romanovsky VE, Stone RS, Stow DA, Sturm M, Tweedie CE, Vourlitis GL, Walker MD, Walker DA, Webber PJ, Welker JM, Winker KS, and Yoshikawa K. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change* **72**: 251-298.

Intergovernmental Panel on Climate Change. 2001. *Climate change 2000, third assessment report.* Cambridge University Press: Cambridge.

Intergovernmental Panel on Climate Change (IPCC). 2001. *Climate change 2000, third assessment report.* Cambridge University Press: Cambridge.

Johannessen OM, Bengtsson L, Miles MW, Kuzmina SI, Semenov VA, Alekseev GV, Nagurnyi AP, Zakharov VF, Bobylev LP, Pettersson LH, K. H, and Cattle HP. 2004. Arctic climate change: observed and modeled temperature and sea-ice variability. *Tellus* **56A**: 328-341.

Johnson AW, and Neiland BJ. 1983. An analysis of plant succession on frost scars 1961-1980. Proceedings on Permafrost: Fourth International Conference. National Academy Press: University of Alaska Fairbanks, Fairbanks.

Jonasson S, and Sköld SE. 1983. Influences of frost-heaving on vegetation and nutrient regime of polygon-patterned ground. *Vegetatio* **53**: 97-112.

Kade A, Walker DA, and Raynolds MK. 2005. Plant communities and soils in cryoturbated tundra along a bioclimate gradient in the Low Arctic, Alaska. *Phytocoenologia* **35**: in press.

Klene AE, Nelson FE, and Shiklomanov NI. 2001. The n-factor as a tool in geocryological mapping: seasonal thaw in the Kuparuk River Basin, Alaska. *Physical Geography* **22**: 449-466.

Luthin JN, and Guymon GL. 1974. Soil moisture-vegetation-temperature relationships in central Alaska. *Journal of Hydrology* **23**: 233-246.

Michaelson GJ, Ping CL, Kling GW, and Hobbie JE. 1998. The character and bioactivity of dissolved organic matter at thaw and in the spring runoff waters of the arctic tundra North Slope, Alaska. *Journal of Geophysical Research* **103**: 28,939-928,946.

Michaelson GJ, Ping CL, and Walker DA. 2005. Biogeochemistry of soils associated with cryptogamic crusts on frost boils in arctic Alaska. *Arctic, Antarctic and Alpine Research*: (in review).

Nelson FE, Hinkel KM, Shiklomanov NI, Mueller GR, Miller LL, and Walker DA. 1998. Active-layer thickness in north central Alaska: systematic sampling, scale, and spatial autocorrelation. *Journal of Geophysical Research* **103**: 28,963-928,973.

Onset Computer Corporation. 2000. Hobo H8 Pro Series. Onset Computer Corporation: Bourne.

Osterkamp TE, and Romanovsky VE. 1999. Evidence for warming and thawing of discontinuous permafrost in Alaska. *Permafrost and Periglacial Processes* **10**: 17-37.

Pavlov AV, and Moskalenko NG. 2002. The thermal regime of soils in the north of Western Siberia. *Permafrost and Periglacial Processes* **13**: 43-51.

Peterson RA, and Krantz WB. 1998. A linear stability analysis for the inception of differential frost heave. In *Proceedings of the Seventh International Conference on Permafrost*, Yellowknife, Canada; 883-889.

Peterson RA, and Krantz WB. 2003. A mechanism for differential frost heave and its implications for patterned ground formation. *Journal of Geology* **49**: 69-80.

Ping CL, Bockheim JG, Kimble JM, Michaelson GJ, and Walker DA. 1998. Characteristics of cryogenic soils along a latitudinal transect in Arctic Alaska. *Journal of Geophysical Research* **103**: 28917-28928.

Ping CL, Michaelson GJ, Kimble JM, Shur YL, and Walker DA. 2002. Morphogenesis of soils associated with frost boils. *Eos Transactions AGU* **83**: Supplement F259.

Popov MV, Kachurin SP, and Grave NA. 1963. Features of the development of frozen geomorphology in northern Eurasia. In *Proceedings of Permafrost International Conference*, Lafayette; 43-50.

Price LW. 1971. Vegetation, microtopography, and depth of active layer on different exposures in subarctic alpine tundra. *Ecology* **52**: 638-647.

SAS Institute Inc. 2004. *The SAS system for Windows V8*. SAS Institute: Cary.

Sigafoos RS. 1951. Soil instability in tundra vegetation. *Ohio Journal of Science* **6**: 281-298.

Sturm M, Schimel J, Michaelson G, Welker JM, Oberbauer SF, Liston GE, Fahnestock J, and Romanovsky VE. 2005. Winter biological processes could help convert arctic tundra to shrubland. *BioScience* **1**: 17-26.

Tukey JW. 1953. *The problem of multiple comparisons*. Princeton University Press: Princeton, N.J.

Walker DA, Auerbach NA, Bockheim JG, Chapin FS, III, Eugster W, King JY, McFadden JP, Michaelson GJ, Nelson FE, Oechel WC, Ping CL, Reeburg WS, Regli S, Shiklomanov NI, and Vourlitis GL. 1998. Energy and trace-gas fluxes across a soil pH boundary in the Arctic. *Nature* **394**: 469-472.

Walker DA, Bockheim JG, Chapin FS, III, Eugster W, Nelson FE, and Ping CL. 2001. Calcium-rich tundra, wildlife, and the "Mammoth Steppe". *Quaternary Science Reviews* **20**: 149-163.

Walker DA, Epstein HE, Gould WA, Kelley AM, Kade A, Knudson JA, Krantz WB, Michaelson GJ, Peterson RA, Ping CL, Raynolds MK, Romanovsky VE, and

Shur Y. 2004. Frost-boil ecosystems: complex interactions between landforms, soils, vegetation and climate. *Permafrost and Periglacial Processes* **15**: 171-188.

Walker DA, Jia GJ, Epstein HE, Raynolds MK, Chapin FS, III, Copass C, Hinzman LD, Knudson JA, Maier HA, Michaelson GJ, Nelson F, Ping CL, Romanovsky VE, and Shiklomanov N. 2003. Vegetation-soil-thaw-depth relationships along a low-arctic bioclimate gradient, Alaska: synthesis of information from the ATLAS studies. *Permafrost and Periglacial Processes* **14**: 103-123.

Walker MD, Walker DA, and Auerbach NA. 1994. Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska. *Journal of Vegetation Science* **5**: 843-866.

Washburn AL. 1980. *Geocryology: A survey of periglacial processes and environments*. John Wiley and Sons: New York.

Williams PJ, and Smith MW. 1989. *The frozen earth: fundamentals of geocryology*. Cambridge University Press: Cambridge.

Zoltai SC, and Tarnocai C. 1981. Some nonsorted patterned ground types in northern Canada. *Arctic and Alpine Research* **13**: 139-151.

Table 4.1. Mean summer temperature (MST), winter temperature (MWT) and annual temperature (MAT) at the soil surface, mean thaw depth, frost heave, snow depth and index of soil-surface instability for the last year of the experiment (2004/2005). Means are shown with standard error in parentheses, and significant differences between treatments as indicated by Tukey pairwise comparisons are noted with different letters (α=0.05).

Response variable	Treatment			
	Veg. removal	Sedges	Mosses	Control
$MST_{soil\text{-}surface}$ (°C)	8.2^{a} (0.3)	7.9^{ab} (0.1)	3.9^{c} (0.3)	6.7^{b} (0.4)
$MWT_{soil\text{-}surface}$ (°C)	-18.7^{b} (0.4)	-17.5^{ab} (0.3)	-16.5^{a} (0.4)	-17.8^{ab} (0.5)
$MAT_{soil\text{-}surface}$ (°C)	-6.5^{a} (0.2)	-6.2^{a} (0.1)	-6.7^{a} (0.2)	-6.6^{a} (0.2)
Thaw depth (cm)	82.4^{a} (0.5)	77.0^{b} (1.0)	66.0^{c} (0.6)	77.6^{b} (0.6)
Frost heave (cm)	15.9^{a} (0.5)	13.3^{b} (0.4)	6.0^{c} (0.4)	12.6^{b} (0.6)
Snow depth (cm)	25.9^{a} (2.9)	22.4^{ab} (0.8)	15.7^{b} (2.1)	19.1^{ab} (1.1)
Index of soil instability	48.1^{a} (0.4)	24.9^{b} (1.6)	2.0^{d} (0.4)	6.6^{c} (1.4)

Table 4.2. Dates of soil freezing and thawing at 1 cm depth for the four treatments.

		Treatment			
		Veg. removal	Sedges	Mosses	Control
Freeze-up	2002	04-Oct-02	04-Oct-02	10-Oct-02	05-Oct-02
	2003	06-Oct-03	05-Oct-03	12-Oct-03	04-Oct-03
	2004	13-Sep-04	13-Sep-04	20-Sep-04	14-Sep-04
Thaw	2003	01-Jun-03	01-Jun-03	12-Jun-03	03-Jun-03
	2004	22-May-04	23-May-04	06-Jun-04	22-May-04
	2005	27-May-05	28-May-05	10-Jun-05	28-May-05

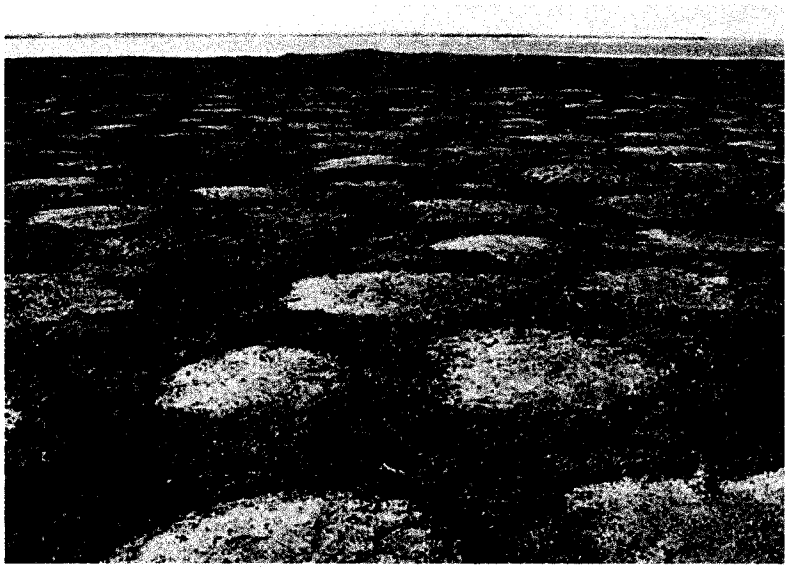

Fig. 4.1. Nonsorted circles dotting the arctic tundra at Howe Island, Alaska.

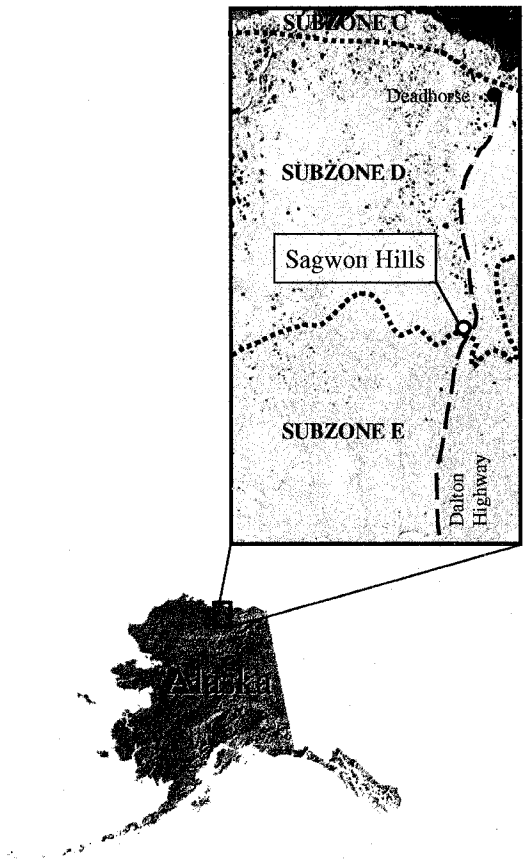

Fig. 4.2. Location of the study site and the climatic subzones along the northern end of the Dalton Highway, Alaska.

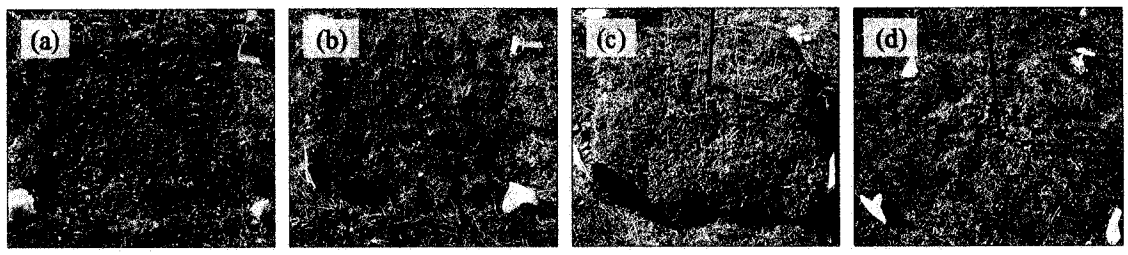

Fig. 4.3. The four treatment groups of the nonsorted circles. (a) Vegetation removal. (b) Sedge transplants. (c) Moss transplants. (d) Control. The plots measure 0.5 m^2.

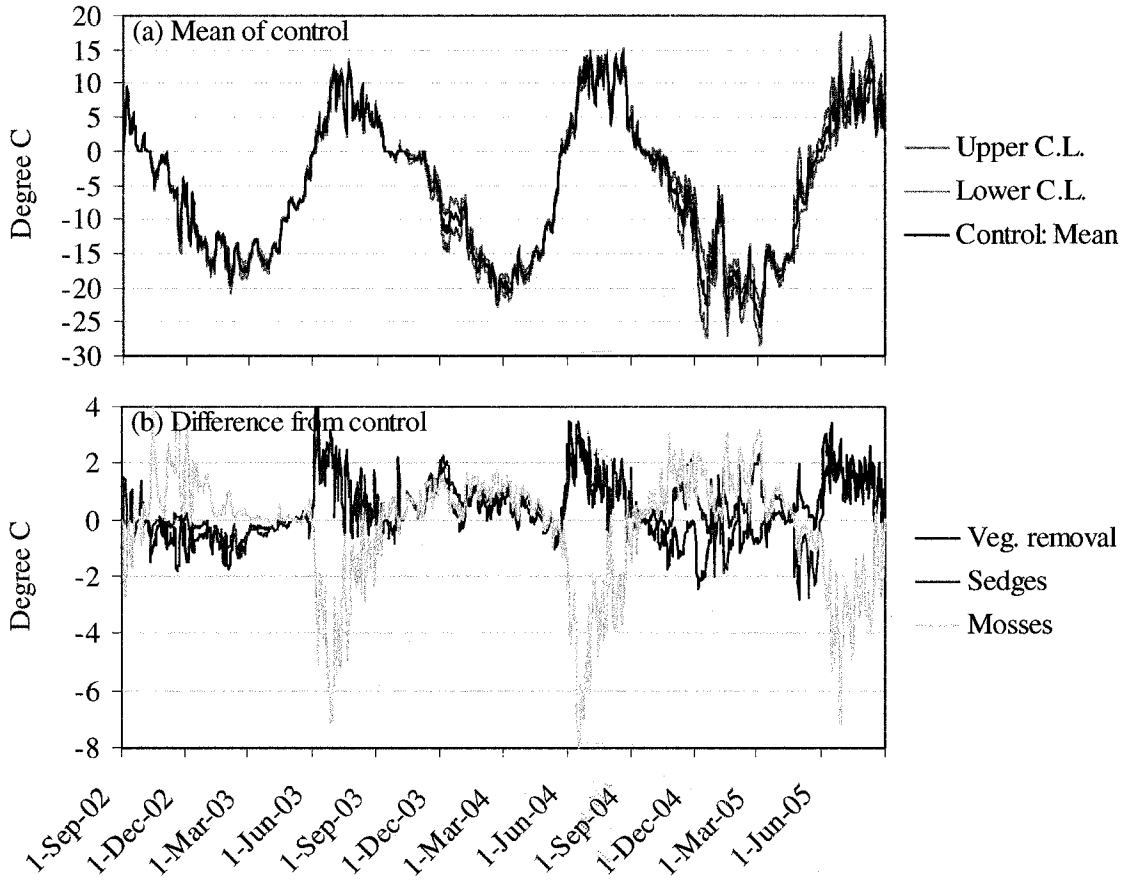

Fig. 4.4. Near-surface soil temperatures (°C) from September 2002 through August 2005. (a) Daily mean temperatures for the control plots, with upper and lower confidence limits. (b) Residuals of the daily mean temperatures for the three vegetation manipulations with respect to the control.

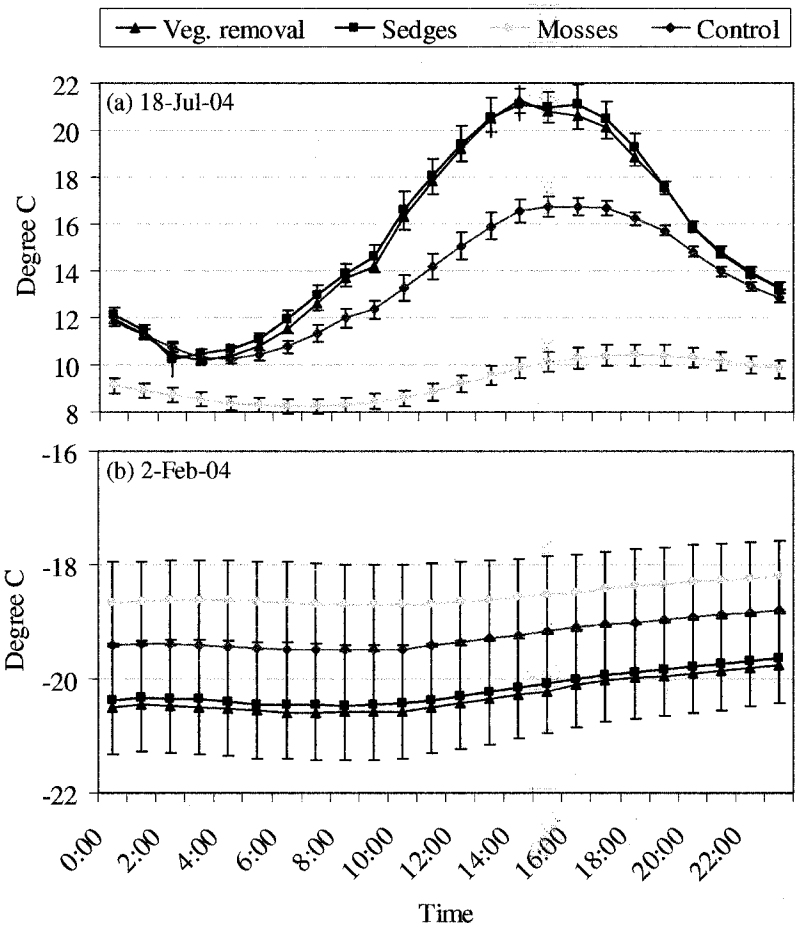

Fig. 4.5. Hourly mean soil temperatures (°C) at 1 cm depth for the four treatments, shown with standard errors. (a) A typical day in the summer. (b) A typical day in the winter.

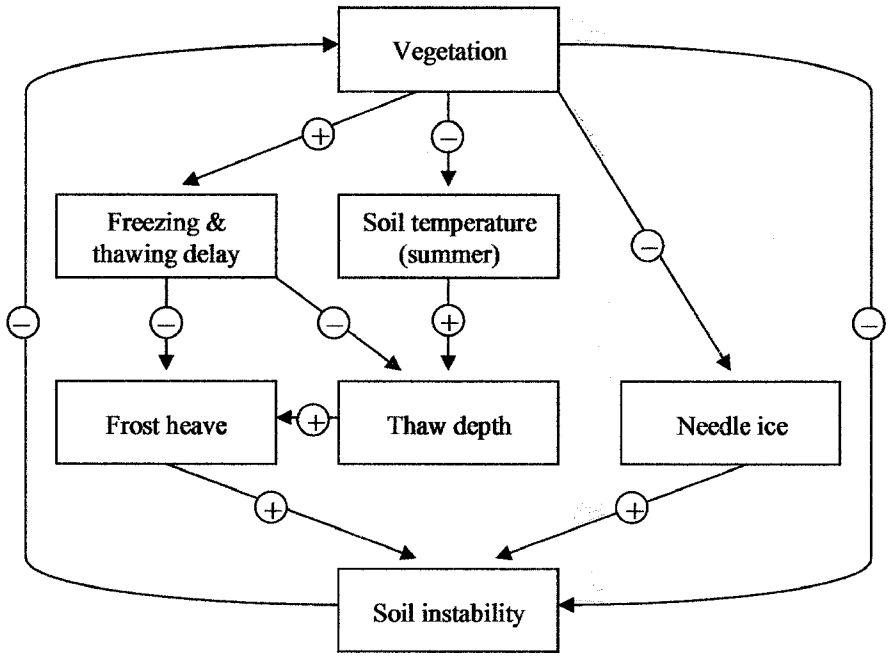

Fig. 4.6. Conceptual model of positive and negative feedbacks among the major variables driving the cryogenic regime of the manipulated nonsorted circles.

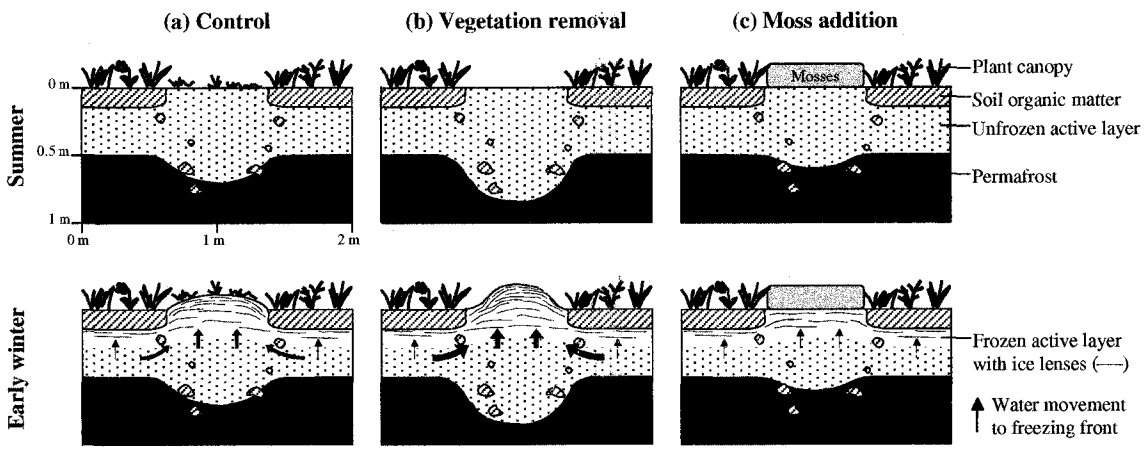

Fig. 4.7. Idealized cross-section of nonsorted circles showing the thaw depth in the summer and the frozen active layer with ice lenses, water movement due to cryostatic suction, and frost heave in early winter during freeze-up. (a) Slightly vegetated nonsorted circle (control treatment). The sedge treatments show responses similar to the control. (b) Bare nonsorted circle after vegetation removal. (c) Nonsorted circle with the addition of a moss carpet. Note the deeper thaw beneath the barren nonsorted circle and the shallower thaw beneath the moss carpet with entrapment of both solid organic matter and dissolved organic carbon in the aggrading permafrost table. The bare surface heaves more than the control, and the moss carpet prevents differential heave of the nonsorted circle. The size of the arrows depicting water movement to the freezing front corresponds to the strength of the effect.

CHAPTER 5: SYNTHESIS

This thesis examined the interactions among the vegetation, soils and cryogenic processes of nonsorted circles and the surrounding stable tundra in arctic Alaska. I investigated the biotic and abiotic relationships at the microscale at several study sites and compared the sites along a climate gradient spanning 130 km from the coast of the Arctic Ocean to the Arctic Foothills of the Brooks Range. Here, I (a) summarize the major findings of my thesis, (b) discuss the effects of nonsorted circles on the ecosystem, (c) examine the implications of a warming arctic climate, and (d) give suggestions for further research.

PROPERTIES OF NONSORTED CIRCLES ALONG THE CLIMATIC GRADIENT

The vegetation, soil and cryogenic properties differ between nonsorted circles and the adjacent tundra, and the properties change along a climate gradient from north to south. These properties and their change along the climate gradient are shown for the nonsorted circles in Table 5.1 and for the stable tundra in Table 5.2, and the major points are discussed below. The information presented in the tables is the basis for vegetation-change studies, and ecological modelers can use the results to predict future changes to tundra ecosystems (Epstein *et al.*, 2000). I also examine the original hypotheses stated in the Introduction regarding the response of the nonsorted-circle system along the arctic bioclimate gradient.

Vegetation

I identified and described five associations and four plant community types. Three associations are new. The unit names from north to south are: *Braya purpurascens-Puccinellia angustata* community (dry nonsorted circles, subzone C); *Dryas integrifolia-Salix arctica* community (dry tundra, subzone C); Salici rotundifoliae-Caricetum aquatilis ass. nov. (moist coastal tundra, subzone C); Junco biglumis-Dryadetum integrifoliae ass. nov. (moist nonsorted circles, subzone D); Dryado integrifoliae-Caricetum bigelowii Walker et al. 1994 (moist tundra, subzone D); *Scorpidium scorpioides-Carex aquatilis* community (wet tundra, subzone D); Cladino-Vaccinietum vitis-idaeae ass. nov. (dry nonsorted circles and earth hummocks, subzone E); Sphagno-Eriophoretum vaginati Walker et al. 1994 (moist tundra, subzone E); and *Anthelia juratzkana-Juncus biglumis* community (wet nonsorted circles, subzone E). An ordination analysis revealed that the most important environmental factors resulting in the characteristic species composition of the community types are disturbance through cryoturbation, climate, soil pH and soil moisture.

The nonsorted circles support plant communities that vary distinctly from the adjacent tundra in species composition, plant functional types and vegetation structure. Although all the communities are dominated by nonvascular species, the nonsorted circles are dominated by extremely low-growing lichens and liverworts, whereas the stable tundra areas have more vertical structure with more dwarf shrubs, sedges and a thick moss layer. As the nonsorted circles become more vegetated towards the south and exhibit less bare soil, the cover of dwarf shrubs, graminoids and mosses increases from

0.3%, 0.8% and 3.2% to 37.3%, 12.0% and 59.4%, respectively. Towards the south, fruticose lichens become more dominant, whereas the cover of crustose lichens declines rapidly. In the stable tundra, the average height of the vegetation increases towards the south due to the increased cover of erect dwarf shrubs and graminoids from 0% and 0.9% to 29.5% and 40.1%, respectively. In contrast, the cover of low growing prostrate dwarf shrubs and forbs declines from 81.0% and 6.1% to 12.5% and 2.6%. The changes in community structure have major implications for the thermal regimes of the soils, as will be summarized later in this discussion.

In each subzone, total species richness (alpha diversity) is greater for the nonsorted circles than the adjacent tundra, which is mostly due to a greater diversity of lichens and acrocarpous mosses on the nonsorted circles. The total species number for nonsorted circles and the stable tundra, respectively, is 48 and 34 in subzone C, 164 and 155 in subzone D, and 100 and 78 in subzone E. The species richness of the dominant growth forms for both nonsorted circles and the stable tundra is greatest in subzone D. Only cold-adapted species are able to grow in the harsh climate in subzone C, and competition for light and nutrients probably restricts species establishment in the acidic tundra in subzone E.

The morphology of the nonsorted circles changes along the climatic gradient due to changes in vegetation properties and cryogenic activity. Large, barren nonsorted circles dominate the dry northern sites in subzone C, and they differ greatly in species composition from the adjacent tundra areas. Farther south in subzone D, the relatively barren nonsorted circles support plant communities similar to the northern sites, and the

more stable, vegetated nonsorted circles represent a successional stage between the adjacent stable tundra and the bare circles. Well-vegetated, less active nonsorted circles and earth hummocks dot the southern end of the climate gradient in subzone E. The earth hummocks have thick vegetation mats that resemble the adjacent tundra areas in species composition.

Soil

The soil characteristics are influenced by the plant communities and cryogenic activity. Nonsorted circles usually have more bare ground, thinner organic horizons and lower soil moisture than the surrounding tundra. The nonsorted circles are also strongly associated with moist nonacidic tundra (Walker *et al.*, 1994; Bockheim *et al.*, 1998; Walker *et al.*, 1998), and feedback mechanisms may help maintain the high soil pH due to cryoturbation. At the northern sites, the nonsorted circles have slightly higher pH values and lower total carbon and nitrogen contents than the stable tundra, which can be explained by less plant biomass on the nonsorted circles and therefore less decomposable material and input of leached organic acids into the soils. The soils of nonsorted circles have generally slightly greater bulk densities due to greater clay contents and less coarse-textured particles. This indicates that even in these fine-grained soils sorting caused by frost heave is moving coarser materials to the edges of the nonsorted circles.

The soil chemical properties also change along the climate transect. The soils at the northern end of the gradient are nonacidic with a pH of 8.3 ± 0.1 in the nonsorted circles and 7.9 ± 0.1 in the stable tundra, whereas the soils towards the south in the Arctic

Foothills have a pH of 5.2 ± 0.1 in the active circles and 5.3 ± 0.1 in the stable tundra. There is a clear boundary between the acidic and nonacidic regions at the northern edge of the Arctic Foothills (Bockheim *et al.*, 1998; Walker *et al.*, 1998), and the causes of the pH boundary are still not fully understood. The soils at the southern sites may experience more leaching due to greater precipitation, and the leached soils have a low pH. One hypothesis for the large differences is that the windier climate north of the Arctic Foothills is responsible for greater evapotranspiration and less snow accumulation, leading to a higher soil pH. The soils in the nonacidic tundra are richer in plant-available nutrients than the acidic soils, supporting a different suite of plant species.

Cryogenic processes

The thick vegetation mats and soil organic horizons on the stable tundra act as an insulative layer, resulting in cooler summer temperatures at the mineral soil surface and delaying thawing and freezing of the soil when compared to the nonsorted circles. The active layer of the stable tundra is shallow, decreasing the amount of ice-lens formation and thus frost heave in the winter. In contrast, the nonsorted circles have warmer summer and cooler winter temperatures at the soil surface due to the minimal insulation provided by the thin vegetation mats and organic horizons and the shallow snow cover. In the summer, the warm soils of the nonsorted circles allow for deeper thaw depths and the formation of more ice lenses and thus greater frost heave in the winter when compared to the stable tundra. The partially vegetated nonsorted circles in subzone D and the small bare circles in subzone E show substantial differential frost heave, heaving 13 to 15 cm

more than the adjacent stable tundra. In subzone C, the bare nonsorted circles are well expressed but show only little differential heave. The thinly vegetated stable tundra areas do not differ much in soil thermal properties and thaw depth from the nonsorted circles, apparently suppressing cryostatic suction and differential heave. The heave may also be negatively affected by the sandy soils at Howe Island, as heave is thought to be most strong in silty soils and minimum in sands (Peterson and Krantz, 2003). The vegetation may be absent from these circles not due to differential heave but high needle-ice activity and high salt concentrations in the circle soils (Michaelson *et al.*, 2005). In all subzones, the soils of the nonsorted circles experience less soil-surface stability than the adjacent stable tundra due to frost heaving and possibly the formation of needle ice, especially in bare circles. This in turn prevents plant succession and the formation of a continuous insulative vegetation mat, thus reinforcing cryogenic processes.

The modified n-factor (n'-factor), which is a simple indicator of the energy balance at the soil surface, is defined as the ratio of seasonal thawing degree-day sums at the soil surface to that in the air (Carlson, 1952). It is greater for nonsorted circles than the stable tundra, and it decreases along the climate gradient from north to south from 1.4 to 0.4 at the nonsorted circles and from 1.0 to 0.2 at the adjacent tundra. This is the result of greater thermal insulation at the soil surface provided by a thicker, more continuous vegetation cover and a thicker soil organic and snow layer. The n'-factor is closely linked to the thaw depth, which generally decreases from north to south.

Interactions among system components along the bioclimate gradient

The elements of the nonsorted-circle system (vegetation, soil, cryogenic regime) interact with each other through (1) litter input from the vegetation to the soil and the availability of mineralized nutrients in the soil, (2) dampening of the cryogenic processes due to insulation of the vegetation and soil organic layer, and (3) disturbance of the vegetation and soil organic mat as well as churning of soil organic matter due to cryogenic action (Fig. 5.1). The dominance of each component in the system and the strengths of these interactions change along the arctic bioclimate gradient, as hypothesized earlier. In the north in subzone C, the physical processes determining the cryogenic activity (such as frost heave, thaw depth, soil churning and soil-surface stability) are dominant in the nonsorted circles and create barren areas, while biological interactions between the continuous vegetation mat and soil are dominant in the stable tundra. Similarly, cryogenic activity dominates the nonsorted circles in subzone D and maintains disturbed soils with great differential heave, creating a strong contrast to the well-vegetated stable tundra. In subzone E, the warm climate favors thicker vegetation mats on and off the less active nonsorted circles, and cryogenic processes are less dominant. The contrast between nonsorted circles and the stable tundra is minimal. The strength of the interactions may change under a warming arctic climate, as discussed below.

EFFECTS OF NONSORTED CIRCLES ON THE ECOSYSTEM

The nonsorted-circle system within the arctic tundra shows interactions among vegetation, soil and cryogenic regime. At the ecosystem scale, nonsorted circles are linked to several components of the greater arctic system (Fig. 5.2), which are discussed here.

Germination, and plant and landscape diversity

The nonsorted circles in the climate subzones C and D experience strong disturbances at the soil surface caused by frost heave and needle-ice formation. This disturbance reduces plant establishment (Johnson and Neiland, 1983; Anderson and Bliss, 1998) and delays successional trends (Sigafoos, 1951; Haugland and Beatty, 2005). However, the soil disturbance may also be important in providing the main opportunity for the regeneration of certain seedlings (Gartner *et al.*, 1986; Gough, 2006). Gough (2006) performed field transplants and germination experiments with neighbor removal in Alaskan arctic tundra and found that species interactions may restrict germination. Bare ground was required for the recruitment of new individuals, and plants in densely vegetated areas showed only clonal growth.

The soil disturbance through cryogenic action also creates arid soil conditions within a region with relatively humid conditions by transforming the microclimate (Goryachkin *et al.*, 1999). As a result, the dry, disturbed nonsorted circles are colonized by distinctly different plant communities than the stable moist tundra. For example, the *Braya purpurascens-Puccinellia angustata* community and the Junco biglumis-

Dryadetum integrifoliae association of the dry nonsorted circles in subzone C and D, respectively, support numerous small herbs (e.g. *Braya purpurascens*, *Puccinellia angustata*), mosses (*Bryum wrightii*) and lichens (e.g. *Lecanora epibryon*, *Polyblastia sendtneri*) that are absent of less common in the stable tundra. Whittaker (1965) made a distinction between two types of diversity, with alpha diversity describing the number of species within a chosen area or community and beta diversity being the diversity of communities across the landscape. The different plant species and abundances found in the communities of the nonsorted circles increase the beta diversity and heterogeneity of the arctic tundra landscape, with the nonsorted circles acting as distinct landscape patches within the stable tundra matrix. Raynolds *et al.* (2005) mapped the vegetation patterns of nonacidic and acidic tundra in northern Alaska and found greater beta diversity in the nonacidic tundra than in the acidic tundra due to the abundance of nonsorted circles. Similarly, Haugland and Beatty (2005) stated that frost disturbance in patterned ground in Norway delays successional trends, and that the small disturbed patches are important with respect to vegetation assemblages across the landscape.

Permafrost and active layer

The arctic tundra is underlain by permanently frozen ground, which blocks the downward growth of plant roots. The permafrost also hinders the downward seepage of water, thus affecting the conditions for biological and biogeochemical processes in the active layer above by creating reduced conditions due to saturation (Ping *et al.*, 1998). Events that cause the top of the permafrost table to melt can lead to thermokarsting

(Williams and Smith, 1989; Osterkamp and Romanovsky, 1999). When compared to the stable tundra, the nonsorted circles have warmer soil temperatures in the summer along with deeper active layers, and colder soil temperatures in the winter. However, the mean annual soil-surface temperatures are similar for nonsorted circles and adjacent tundra. The vegetation, soil organic horizon and snow have a large effect on the active layer but apparently have a minimal overall net effect on the local annual soil-surface temperature regime, suggesting that the overall permafrost temperatures are also not be affected by the presence of vegetation or nonsorted circles.

Arctic ecosystems depend on the active layer of the soil, which is the top layer of the ground that thaws and freezes annually and overlays the permafrost. The active layer is important to key biological, biogeochemical, hydrological and soil-forming processes (Hinzman *et al.*, 1998; Ping *et al.*, 2002), and its thickness is directly related to surface temperatures in the summer. The barren to thinly vegetated nonsorted circles experience higher soil-surface temperatures in the summer and have greater thaw depths than the adjacent stable tundra (chapter 3; Kelley *et al.*, 2004). A thicker active layer within the nonsorted circles improves the drainage above the permafrost table and results in drier, warmer soils in the summer and more oxidized conditions than the surrounding tundra (Michaelson *et al.*, 1998; Ping *et al.*, 2002).

Nitrogen cycling and carbon storage

Nonsorted circles support cryptobiotic crusts composed of lichens, small mosses, liverworts and algae (Michaelson *et al.*, 2005). These crusts are of considerable

importance for stabilizing the barren soils. In addition, the algae crusts are important because of their nitrogen fixation in a system that is generally nitrogen-limited. The nitrogen dynamics differ between nonsorted circles and the surrounding tundra. Kelley (pers. comm.) found greater nitrogen contents and rates of net nitrogen mineralization in stable tundra soils than nonsorted circles. She attributes these differences to the greater organic matter content in the stable tundra with greater microbial-driven nitrogen mineralization and immobilization rates than in the nonsorted circles. Similarly, Hobbie and Gough (2002) reported higher rates of net nitrogen mineralization from moist acidic arctic tundra soils with thick organic horizons when compared to the moist nonacidic tundra with thinner organic horizons and a greater abundance of bare nonsorted circles.

The cryogenic action, mainly frost heave, of the nonsorted circles results in soil churning and downward movement of surface organic matter through the soil profile. The organic matter gets incorporated into the lower active layers and eventually into the upper permafrost, leading to the sequestration of organic carbon (Bockheim *et al.*, 1998; Ping *et al.*, 1998). Ping *et al.* (2005) found consistently greater organic carbon stores in nonsorted-circle soils than the stable tundra. They also reported an increasing degree of churning of soil organic matter and carbon sequestration associated with increasing age of the nonsorted circles.

Trace-gas and energy fluxes

The bare, relatively dry nonsorted circles have greater ground heat flux and lower CO_2 uptake and methane emissions than the stable tundra. Eugster *et al.* (2005) and

Walker *et al.* (1998) found that the moist acidic tundra in Alaska has greater aerodynamic roughness, less ground heat flux, greater CO_2 uptake and higher methane emissions than the moist nonacidic tundra. Although these studies did not specifically focus on nonsorted circles, the differences in trace-gas and energy fluxes are associated with the greater amounts of bare soil in the nonacidic tundra due to the abundance of nonsorted circles.

Hydrology

The thick vegetation and organic layers and the shallow thaw depth of the stable tundra act as a buffer to the downward movement of water and dissolved chemicals, while the relatively bare nonsorted circles experience larger fluxes of water. The solute concentrations increase with depth and are greatest at the top of the permafrost table (Kokelj and Burn, 2003). Boike (pers. comm.) reports slightly higher solute concentrations in the bowl-shaped region beneath nonsorted circles, which depress the freezing point and may contribute to the formation and maintenance of patterned-ground. Nonsorted circles also experience water redistribution during freeze-up. Bare nonsorted circles can heave 20 cm (Romanovsky, unpublished data), which is up to 10 times larger than the heave expected by the 9% volume increase when soil water freezes. The additional water moves from the stable tundra areas to the nonsorted circles. This is also supported by the experimental removal of vegetation on nonsorted circles in the Alaskan arctic tundra and the resulting increase in frost heave, with the excess water for ice-lens

formation coming from the adjacent tundra areas, possibly either through the slow movement of ground water or through cryostatic suction (Kade and Walker, 2005).

Animal use

The cryoturbation activity associated with nonsorted circles exposes calcareous mineral soil and prevents the buildup of thick organic horizons, which is important to both plant communities and wildlife. Plants on the nonsorted circles and surrounding stable areas of the nonacidic tundra have great concentrations of leaf-tissue calcium (Bockheim *et al.*, 1998), which promotes the bone development and lactation of mammals (Walker *et al.*, 2001). The nonsorted circles of the moist nonacidic tundra increase the plant species diversity of the area and allow for warmer soils in the summer, resulting in greater activity patterns of certain microarthropod species (Gonzalez, pers. comm.), and greater numbers of both small mammals, such as voles, ground squirrels and lemmings, and large mammals, such as caribou, muskoxen and grizzly bears (Walker *et al.*, 2001). Nonsorted circles support greater amounts of *Cetraria* and *Cladonia* species than the adjacent tundra, which are among the most important forage species for caribou (Scotter, 1965) and should affect their foraging patterns.

Human disturbance

Several studies have investigated the impact of human disturbance such as off-road vehicle traffic (as opposed to the natural soil disturbance created by nonsorted circles) on tundra plant communities. Chapin and Shaver (1981) and Walker *et al.* (1987)

found warmer soils with deeper thaw and increased plant productivity following tundra disturbance by vehicles. The community composition differed between disturbed and undisturbed tundra, with more graminoids and less shrubs and forbs growing in the disturbed sites. This negative response of shrubs, particularly ericaceous and evergreen shrubs, to vehicle-track disturbance is similar to that of plant communities found on cryoturbated nonsorted circles, which are poor in shrubs. However, the dry nonsorted circles often do not support more graminoids than the stable tundra, whereas the water-rich channels created by the vehicle tracks are favorable microsites for sedges. Off-road vehicle use in dry tundra leads site conditions similar to the naturally disturbed nonsorted circles, with initial establishment of mosses and lichens and slow invasion by vascular plants (Everett *et al.*, 1983). Emers *et al.* (1995) also found that nonsorted circles experience higher levels of disturbance by seismic activity because of the greater microtopography when compared to the stable tundra.

IMPLICATIONS OF CLIMATE CHANGE

The climate of the Arctic is changing (e.g. Chapin *et al.*, 2004; Johannessen *et al.*, 2004; Hinzman *et al.*, 2005), and a significant warming trend over the last 30 years has been reported by Serreze *et al.* (2000). The interactions among the system components of the cryoturbated tundra are strongly controlled by the regional climate, and nonsorted circles should be highly susceptible to climatic change as they seem to form only under certain environmental conditions (Walker *et al.*, 2004). The potential effects of a

warming climate on the major drivers of the patterned-ground system are discussed below.

The morphology of nonsorted circles is strongly controlled by climate (Chernov and Matveyeva, 1997; Walker *et al.*, 2004), and the processes controlling the landscape change along the climate gradient (Fig. 5.1, see discussion above). Under a warming climate, the dominant processes acting on the landscape might shift northwards, and increased biomass and shift in vegetation zones and species composition have been predicted (Chapin *et al.*, 1995; Epstein *et al.*, 2000). The contrast in vegetation characteristics between the stable tundra and the nonsorted circles influences the cryogenic activity through the differences in soil thermal properties, thaw depth, amounts of ice lenses and resulting differential frost heave. A warming climate might lead to vegetation shifts both on and off the nonsorted circles and change the degree of contrast, influencing the feedbacks with the cryogenic regime. The potential changes in vegetation and morphology under a warming climate should vary along the climate gradient, as shown in Fig. 5.3. In addition, several system properties such as biomass, the depth of the organic horizon, nutrient availability, heat flux as indicated by the n'-factor, thaw depth and frost heave may respond to a warming climate. The anticipated response patterns of these variables on and off the nonsorted circles along the climate gradient are shown in Fig. 5.4. The trends in Fig. 5.3 and Fig. 5.4 are discussed below.

In the north in subzone C, the physical constraints of the harsh environment result in low plant cover, biomass and thin organic horizons on the stable tundra, and the nonsorted circles remain mostly barren due to high needle-ice activity and high salt

concentrations in the soils. Warmer temperatures could favor thicker moss mats on the stable tundra (Walker *et al.*, 2003), increase the amount of available nutrients and reduce the n'-factor and thaw depth. Walker *et al.* (2004) found no relationship between frost heave and plant biomass on the stable tundra, and frost heave should remain similar. Pioneer species might colonize the edges of the nonsorted circles, which may heave differentially more than the stable tundra due to an increasing contrast in biomass between the circles and the stable tundra. A minimal increase in plant cover and biomass on the nonsorted circles would not lead to great changes in organic matter depth, nutrient availability and n'-factor.

In subzone D, physical processes still constrain the development of continuous vegetation carpets on the active nonsorted circles, which have great heat flux, deep thaw and great differential frost heave. In contrast, biological processes dominate in the surrounding tundra due to the moderate climate, allowing for denser vegetation, thicker organic layers and greater nutrient pools, and reducing heat flux, thaw and heave. Under a warming climate, the nonsorted circles may become masked by thicker vegetation mats and organic horizons, reducing the n'-factor, thaw depth and thus differential frost heave, and resulting in more acidic soils. Also, the formation of needle ice would decrease, increasing soil-surface stability and having a positive feedback on plant succession.

In the south in subzone E, biological processes dominate the landscape morphology and result in poorly developed, well-vegetated nonsorted circles. These features may have developed under a colder climate when there was less vegetation. Under a warmer climate, an increase in biomass and soil organic layer may increase

nutrient availability and reduce the n'-factor, thaw depth and frost heave of nonsorted circles, which would then resemble the adjacent tundra. In some areas, climate change may lead to the conversion of the moss-rich tussock tundra into shrub tundra with overall greater heat flux and thaw depth (Chapin *et al.*, 1995; Epstein *et al.*, 2000; Sturm *et al.*, 2005) and less differential frost heave, potentially resulting in the local disappearance of nonsorted circles and thus decreasing landscape heterogeneity.

A warmer arctic climate and drier soils as predicted under global climate change could favor microbial activity and decomposition rates, thus increasing the rate of nutrient cycling and promoting plant growth on and off the nonsorted circles. More favorable site conditions could also lead to the local decomposition of buried organic material, which is frozen and locked up in the upper permafrost due to cryoturbation and past geologic events, and the release of carbon to the atmosphere (Ping *et al.*, 1998). The increased carbon emissions should have a positive feedback on climate warming. However, the potential release or sequestration of carbon depends strongly on vegetation characteristics. The experimental removal and addition of vegetation on nonsorted circles in northern Alaska resulted in great changes in thaw depths (chapter 4). For example, an increase in thaw depth by 5 cm due to less insulation through vegetation (vegetation removal, chapter 4) might translate to an extra 0.37 kg m^{-2} previously frozen organic carbon that is potentially decomposable. In contrast, a decrease in thaw depth by 11 cm due to an increase in biomass (addition of 10 cm-thick moss carpet, chapter 4) may lead to the potential sequestration of 3.96 kg m^{-2} organic carbon in the upper permafrost.

The potential effect of a warming climate on the temperature regime at the soil surface is not straight forward. Warmer air temperatures and the predicted increase in winter precipitation (Mitchell *et al.*, 1990) should enhance the soil-surface temperatures and result in longer thawing periods, deeper active layers and possibly thermokarsting (Hinzman *et al.*, 2005). However, increased plant growth (Epstein *et al.*, 2000) and thicker soil organic horizons due to a warmer climate would act as an insulative layer, decrease the modified n-factor and thaw depth and possibly lead to permafrost aggradation. In both scenarios, the poorly insulated nonsorted circles have a minimal overall net effect on the annual soil-surface temperature regime and should not affect the temperature of the permafrost table.

SUGGESTIONS FOR FURTHER RESEARCH

This research is part of a larger ongoing project that is extending knowledge of vegetation, soils and cryogenic activity farther north along a climate transect in northern Canada. It is important to examine how the major components driving the ecosystem change along the whole climate gradient from the High to the Low Arctic and to understand the complex linkages among vegetation, microclimate and cryogenic activity in order to predict how these variables may change in response to a warming arctic climate. In addition to expanding the research reported here farther north, several other suggestions for further research are listed here.

Soil-surface temperatures seem to play an important role in predicting cryogenic activity; however, this study examined the soil-surface temperatures and modified n-

factor of three sites over the course of only one year. More long-term data at more sites are needed to confirm the findings reported here.

It would be useful to duplicate the manipulation of the plant canopy on nonsorted circles at several study sites along the full climate gradient in order to quantify the effect on cryogenic activity and compare within versus among site variability. In addition, it would be interesting to manipulate the vegetation of the adjacent stable tundra similar to the experiments conducted by Kokelj (2005). Kokelj (2005) removed the vegetation around earth hummocks at Inuvik, Canada, and recorded the collapse of these frost-heave features as a result of thawing permafrost. The insulating effect of snow in the winter and its influence on cryogenic features could also be studied through experiments. For example, one could examine the effect of addition or removal of snow on the cryogenic activity.

Disturbance at the soil surface seems to be the major factor delaying successional trends on nonsorted circles. This study assumed that the formation of needle ice in the bare soils was mainly responsible for the soil-surface disturbance on nonsorted circles but did not examine needle ice *per se*. More research is needed on the drivers of soil-surface disturbance in order to understand the vegetation responses to cryogenic features.

Although trace-gas and heat-flux measurements have been made in nonacidic tundra and contrasted with those in acidic tundra (Walker *et al.*, 1998; Eugster *et al.*, 2005), a more detailed analysis is needed to determine the flux of individual components (the circle and inter-circle areas) of the system. These fluxes should be examined on and

off nonsorted circles and along a latitudinal gradient to assess the potential impact of a changing climate.

So far, too few studies have linked animal use to nonsorted circles. Gonzalez and Makarova (pers. comm.) examined the diversity and abundance of microarthropods in the Canadian Arctic and found that nonsorted circles provide habitat for certain microarthropod communities. Additional studies could investigate the influence of the barren soils of the nonsorted circles on the activity of small burrowing mammals, and how the lichen and forb-rich plant communities found on nonsorted circles affect the foraging patterns of larger animals such as caribou.

In summary, the nonsorted-circle system shows complex interactions among vegetation patterns, soil properties, cryogenic activity and climate. This thesis examined these interactions by treating nonsorted circles within the stable tundra as a single complex system. I presented a formal description and analysis of the plant communities on and off nonsorted circles along a climatic gradient and placed the plant communities into the larger framework of vegetation orders and classes, laying the foundation for further arctic vegetation classification and vegetation modeling work. I studied the effects of vegetation, soil organic mat and snow on the microclimate of the nonsorted circles and the stable tundra, and I examined how the vegetation affects the cryogenic activity of nonsorted circles with the help of an experiment. I also investigated the changing strength of the interactions among vegetation, soil and cryogenic activity along the bioclimate gradient and discussed the implications for a warming arctic climate.

REFERENCES

Anderson DG, and Bliss LC. 1998. Association of plant distribution patterns and microenvironments on patterned ground in a polar desert, Devon Island, N.W.T., Canada. *Arctic and Alpine Research* **30**: 97-107.

Bockheim JG, Walker DA, and Everett KR. 1998. Soil carbon distribution in nonacidic and acidic tundra of arctic Alaska. In *Soil processes and the carbon cycle*, Lal R, Kimble JM, Follett RF, and Stewart BA (eds). CRC Press: New York.

Carlson H. 1952. Calculation of depth of thaw in frozen ground. Frost action in soils: a symposium. Highway Research Board Special Report 2, National Research Council: Washington, D.C.; 192-223.

Chapin FS, III, Peterson G, Berkes F, Callaghan TV, Angelstam P, Apps M, Beier C, Bergeron Y, Crépin A-S, Danell K, Elmqvist T, Folke C, Forbes B, Fresco N, Juday G, Niemelä J, Shvidenko A, and Whiteman G. 2004. Resilience and vulnerability of northern regions to social and environmental change. *Ambio* **33**: 344-349.

Chapin FS, III, and Shaver GR. 1981. Changes in soil properties and vegetation following disturbance of Alaskan Arctic tundra. *Journal of Applied Ecology* **18**: 605-617.

Chapin FS, III, Shaver GR, Giblin AE, Nadelhoffer KG, and Laundre JA. 1995. Response of arctic tundra to experimental and observed changes in climate. *Ecology* **76**: 694-711.

Chernov YI, and Matveyeva NV. 1997. Arctic ecosystems in Russia. In *Ecosystems of the world, vol. 3: Polar and alpine tundra*, Wielgolaski FE (ed). Elsevier: Amsterdam; 361-507.

Emers M, Jorgenson JC, and Raynolds MK. 1995. Response of arctic tundra plant-communities to winter vehicle disturbance. *Canadian Journal of Botany* **73**: 905-917.

Epstein HE, Walker MD, Chapin FS, III, and Starfield AM. 2000. A transient, nutrient-based model of arctic plant community response to climate warming. *Ecological Applications* **10**: 824-841.

Eugster W, McFadden JP, and Chapin FS, III. 2005. Differences in surface roughness, energy, and CO_2 fluxes in two moist tundra vegetation types, Kuparuk watershed, Alaska, U.S.A. *Arctic, Antarctic and Alpine Research* **37**: 61-67.

Everett KR, Murray BM, Murray DF, Johnson AW, Webber PJ, and Linkins AE. 1983. Long-term environmental adjustment to impact: Cape Thompson, Alaska. Proceedings of the 33rd Alaska Science ConferenceFairbanks, Alaska.

Gartner BL, Chapin FS, III, and Shaver GR. 1986. Reproduction of *Eriophorum vaginatum* by seed in Alaskan tussock tundra. *Journal of Ecology* **74**: 1-18.

Goryachkin SV, Karavaeva NA, Targulian VO, and Glazov MV. 1999. Arctic soils: spatial distribution, zonality and transformation due to global change. *Permafrost and Periglacial Processes* **10**: 235-250.

Gough L. 2006. Neighbor effects on germination, survival, and growth in two arctic tundra plant communities. *Ecography* **29**: 1-13.

Haugland JE, and Beatty SW. 2005. Vegetation establishment, succession and microsite frost disturbance on glacier forelands within patterned ground chronosequences. *Journal of Biogeography* **32**: 145-153.

Hinzman LD, Bettez ND, Bolton WR, Chapin FS, III, Dyurgerov MB, Fastie CL, Griffith B, Hollister RD, Hope A, Huntington HP, Jensen AM, Jia GJ, Jorgenson T, Kane DL, Klein DR, Kofinas G, Lynch AH, Lloyd AH, McGuire AD, Nelson FE, Oechel WC, Osterkamp TE, Racine CH, Romanovsky VE, Stone RS, Stow DA, Sturm M, Tweedie CE, Vourlitis GL, Walker MD, Walker DA, Webber PJ, Welker JM, Winker KS, and Yoshikawa K. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change* **72**: 251-298.

Hinzman LD, Goering DJ, and Kane DL. 1998. A distributed thermal model for calculating soil temperature profiles and depth of thaw in permafrost regions. *Journal of Geophysical Research* **103**: 28,975-928,991.

Hobbie SE, and Gough L. 2002. Foliar and soil nutrients in tundra on glacial landscapes of contrasting ages in northern Alaska. *Oecologia* **131**: 453-462.

Johannessen OM, Bengtsson L, Miles MW, Kuzmina SI, Semenov VA, Alekseev GV, Nagurnyi AP, Zakharov VF, Bobylev LP, Pettersson LH, K. H, and Cattle HP. 2004. Arctic climate change: observed and modeled temperature and sea-ice variability. *Tellus* **56A**: 328-341.

Johnson AW, and Neiland BJ. 1983. An analysis of plant succession on frost scars 1961-1980. Proceedings on Permafrost: Fourth International Conference. National Academy Press: University of Alaska Fairbanks, Fairbanks.

Kade A, and Walker DA. 2005. Vegetation-frost heave interactions of nonsorted circles in the Alaskan Low Arctic. Second European Conference on Permafrost. Terra Nostra, GeoUnion Alfred-Wegener-Stiftung: Potsdam, Germany.

Kelley AM, Epstein HE, and Walker DA. 2004. Role of vegetation and climate in permafrost active layer depth in arctic tundra of northern Alaska and Canada. *Journal of Glaciology and Geocryology* **26**: 269-274.

Kokelj SV, and Burn CR. 2003. Ground ice and soluble cations in near-surface permafrost, Inuvik, Northwest Territories, Canada. *Permafrost and Periglacial Processes* **14**: 275-289.

Kokelj SV, Burn CR, and Tarnocai C. 2005. The structure and dynamics of earth hummocks in the subarctic forest near Inuvik, Northwest Territories, Canada. *Eos Transactions AGU* **86**: Supplement C24A-07.

Michaelson GJ, Ping CL, Kling GW, and Hobbie JE. 1998. The character and bioactivity of dissolved organic matter at thaw and in the spring runoff waters of the arctic tundra North Slope, Alaska. *Journal of Geophysical Research* **103**: 28,939-928,946.

Michaelson GJ, Ping CL, and Walker DA. 2005. Biogeochemistry of soils associated with cryptogamic crusts on frost boils in arctic Alaska. *Arctic, Antarctic and Alpine Research*: (in review).

Mitchell JFB, Manabe S, Meleshko V, and Tokioka T. 1990. Equilibrium climate change and its implications for the future. In *Climate change: the IPCC scientific assessment*, Houghton JT, Jenkins GJ, and Ephraums JJ (eds). Cambridge University Press: Cambridge; 131-172.

Osterkamp TE, and Romanovsky VE. 1999. Evidence for warming and thawing of discontinuous permafrost in Alaska. *Permafrost and Periglacial Processes* **10**: 17-37.

Peterson RA, and Krantz WB. 2003. A mechanism for differential frost heave and its implications for patterned ground formation. *Journal of Geology* **49**: 69-80.

Ping CL, Bockheim JG, Kimble JM, Michaelson GJ, and Walker DA. 1998. Characteristics of cryogenic soils along a latitudinal transect in Arctic Alaska. *Journal of Geophysical Research* **103**: 28917-28928.

Ping CL, Michaelson GJ, Kimble JM, Shur YL, and Walker DA. 2002. Morphogenesis of soils associated with frost boils. *Eos Transactions AGU* **83**: Supplement F259.

Ping CL, Michaelson GJ, Kimble JM, Shur YL, and Walker DA. 2005. Morphogenesis of soils associated with frost boils. *Permafrost and Periglacial Processes*: (submitted).

Raynolds MK, Walker DA, Kade A, and Munger CA. 2005. Small-scale patterned ground in the Arctic: maps of vegetation and thaw depth on a north-south transect. *Eos Transactions AGU* **86**: Supplement C24A-06.

Scotter GW. 1965. Chemical composition of forage lichens from Northern Saskatchewan as related to use by Barren-ground caribou. *Canadian Journal of Plant Science* **45**: 246-250.

Serreze MC, Walsh JE, Chapin FS, III, Osterkamp T, Dyurgerov M, Romanovsky V, Oechel WC, Morison J, Zhang T, and Barry RG. 2000. Observational evidence of recent change in the northern high latitude environment. *Climatic Change* **46**: 159-207.

Sigafoos RS. 1951. Soil instability in tundra vegetation. *Ohio Journal of Science* **6**: 281-298.

Sturm M, Schimel J, Michaelson G, Welker JM, Oberbauer SF, Liston GE, Fahnestock J, and Romanovsky VE. 2005. Winter biological processes could help convert arctic tundra to shrubland. *BioScience* **1**: 17-26.

Walker DA, Auerbach NA, Bockheim JG, Chapin FS, III, Eugster W, King JY, McFadden JP, Michaelson GJ, Nelson FE, Oechel WC, Ping CL, Reeburg WS, Regli S, Shiklomanov NI, and Vourlitis GL. 1998. Energy and trace-gas fluxes across a soil pH boundary in the Arctic. *Nature* **394**: 469-472.

Walker DA, Bockheim JG, Chapin FS, III, Eugster W, Nelson FE, and Ping CL. 2001. Calcium-rich tundra, wildlife, and the "Mammoth Steppe". *Quaternary Science Reviews* **20**: 149-163.

Walker DA, Cate D, Brown J, and Racine C. 1987. Disturbance and recovery of arctic Alaskan tundra terrain. CRREL Report, 87-11, U.S. Army Corps of Engineers.

Walker DA, Epstein HE, Gould WA, Kelley AM, Kade A, Knudson JA, Krantz WB, Michaelson GJ, Peterson RA, Ping CL, Raynolds MK, Romanovsky VE, and Shur Y. 2004. Frost-boil ecosystems: complex interactions between landforms, soils, vegetation and climate. *Permafrost and Periglacial Processes* **15**: 171-188.

Walker DA, Jia GJ, Epstein HE, Raynolds MK, Chapin FS, III, Copass C, Hinzman LD, Knudson JA, Maier HA, Michaelson GJ, Nelson F, Ping CL, Romanovsky VE, and Shiklomanov N. 2003. Vegetation-soil-thaw-depth relationships along a low-arctic bioclimate gradient, Alaska: synthesis of information from the ATLAS studies. *Permafrost and Periglacial Processes* **14**: 103-123.

Walker MD, Walker DA, and Auerbach NA. 1994. Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska. *Journal of Vegetation Science* **5**: 843-866.

Whittaker RH. 1965. Dominance and diversity in land plant communities. *Science* **147**: 250-260.

Williams PJ, and Smith MW. 1989. *The frozen earth: fundamentals of geocryology*. Cambridge University Press: Cambridge.

Table 5.1. Characteristics of nonsorted circles with respect to site factors, vegetation, soil properties, and cryogenic processes along the climate gradient. For subzone E, both bare and vegetated circles are listed. Means with standard errors in parentheses. *Data only from Howe Island, Franklin Bluffs and Happy Valley. **Data from Walker *et al.* 2004.

	Variable	Subzone C	Subzone D	Subzone E	
				bare	vegetated
Site factors	Temperature (°C)*				
	Mean July air	6.2	12.0	13.2	13.2
	Mean January air	-24.3	-29.1	-28.0	-28.0
	Mean July mineral soil	8.6 (0.1)	11.5 (0.2)	9.7 (0.2)	5.5 (0.1)
	Mean January mineral soil	-23.1 (0.2)	-19.9 (0.4)	-9.1 (0.1)	-8.7 (0.3)
	n'-factor (mineral soil)*				
	Summer	1.43 (0.02)	0.97 (0.03)	0.74 (0.01)	0.35 (0.01)
	Winter	0.94 (0.01)	0.73 (0.01)	0.34 (0.01)	0.34 (0.01)
	Snow depth (cm)	8.1 (2.0)	27.0 (1.9)	63.2 (0.9)	39.7 (4.6)
Vegetation	Community name	*Braya purpuras-cens-Puccinellia angustata* comm.	Junco biglumis-Dryadetum integrifoliae ass.	*Anthelia juratz-kana-Juncus biglumis* comm.	Cladino-Vaccinietum vitis-idaeae ass.
	Structure				
	Height of vegetation (cm)	0.3 (0.1)	2.1 (0.3)	2.3 (0.5)	6.1 (1.7)
	Bare soil (%)	55.0 (11.8)	26.3 (4.8)	10.6 (4.2)	1.6 (0.3)
	Dominant growth forms	Lichens	Lichens, dwarf shrubs	Lichens, liverworts	Lichens, mosses, dwarf shrubs
	Composition (% cover/spp. #)				
	Erect dwarf shrubs	0.0/0	0.0/3	3.8/7	19.5/9
	Prostrate dwarf shrubs	0.3/4	2.6/5	5.1/2	17.8/2
	Graminoids	0.8/3	3.1/15	10.7/4	12.0/6
	Forbs	1.5/10	3.2/33	0.1/2	7.0/7
	Foliose lichens	0.1/1	0.4/11	4.5/3	2.5/7
	Fruticose lichens	0.1/3	0.8/23	13.2/15	21.7/36
	Crustose lichens	42.6/7	21.6/9	6.1/1	0.7/1
	Pleurocarpous mosses	0.2/3	0.7/16	4.9/2	28.7/5
	Acrocarpous mosses	3.0/15	4.5/40	8.2/9	30.7/14
	Liverworts	0.1/2	0.3/9	44.0/10	0.3/13
Soil properties	Physical properties				
	Moisture (vol.-%)	28.3 (2.9)	39.2 (0.9)	41.8 (1.3)	35.8 (1.6)
	Depth of O-horizon (cm)	0.0 (0.0)	0.2 (0.1)	0.0 (0.0)	6.4 (1.6)
	Bulk density (g/cm^3)	1.11 (0.04)	1.35 (0.04)	1.13 (0.04)	0.95 (0.05)
	Sand (%)	52.1 (3.3)	44.9 (2.7)	28.6 (1.9)	29.8 (1.4)
	Silt (%)	31.8 (2.3)	34.9 (2.6)	43.6 (1.5)	44.4 (1.1)
	Clay (%)	16.1 (3.9)	20.2 (0.6)	27.8 (1.8)	25.8 (0.8)
	Chemical properties				
	pH	8.3 (0.1)	8.1 (0.1)	5.2 (0.1)	5.0 (0.1)
	Total C (%)	4.77 (0.3)	5.1 (0.21)	2.68 (0.55)	3.73 (0.39)
	Total N (%)	0.11 (0.01)	0.18 (0.01)	0.15 (0.04)	0.21 (0.02)
	Ca (me/100g)	39.8 (1.4)	67.3 (6.7)	6.0 (0.9)	5.4 (0.9)
	Mg (me/100g)	2.35 (0.12)	1.7 (0.18)	1.07 (0.11)	0.76 (0.10)
	K (me/100g)	0.18 (0.01)	0.12 (0.01)	0.08 (0.01)	0.10 (0.01)
	Na (me/100g)	3.18 (0.61)	0.05 (0.01)	0.02 (0.01)	0.02 (0.01)
Cryo. Prc.	Morphology	Bare circles, 1-3 m diameter	Partially veg. circles, 0.5-2 m diameter	Bare circles, 0.5 m diameter	Veg. circles and mounds, 1 m diameter
	Thaw depth (cm)	79.4 (1.1)	88.1 (1.4)	59.8 (1.9)	60.3 (0.9)
	Frost heave (cm)**	4	18	16	9
	Needle-ice activity	High	Intermediate	High	Low

Table 5.2. Characteristics of the stable tundra with respect to site factors, vegetation, soil properties, and cryogenic processes along the climate gradient. Means with standard errors in parentheses. *Data only from Howe Island, Franklin Bluffs and Happy Valley. **Data from Walker *et al.* 2004.

	Variable	Subzone C	Subzone D	Subzone E
Site factors	Temperature (°C)*			
	Mean July air	6.2	12.0	13.2
	Mean January air	-24.3	-29.1	-28.0
	Mean July soil (1 cm)	6.6 (0.1)	4.3 (0.3)	2.4 (0.1)
	Mean January soil (1 cm)	-21.0 (0.2)	-13.5 (0.4)	-7.9 (0.1)
	n'-factor*			
	Summer	0.99 (0.02)	0.35 (0.01)	0.17 (0.01)
	Winter	0.87 (0.01)	0.53 (0.02)	0.32 (0.01)
	Snow depth (cm)	13.3 (2.7)	39.8 (2.5)	60.1 (4.4)
Vegetation	Community name	*Dryas integrifolia-Salix arctica* comm.	Dryado integrifoliae-Caricetum bigelowii ass.	Sphagno-Eriopho-retum vaginati ass.
	Structure			
	Average veg. height (cm)	1.8 (0.2)	5.8 (0.5)	19.4 (2.3)
	Bare soil (%)	0.0 (0.3)	0.3 (0.2)	0.0 (0.0)
	Dominant growth forms	Mosses, dwarf shrubs	Mosses, sedges, dwarf shrubs	Mosses, tussock sedges, dwarf shrubs
	Composition (% cover/spp. #)			
	Erect dwarf shrubs	0.0/0	0.2/7	29.5/8
	Prostrate dwarf shrubs	81.0/4	38.9/5	12.5/2
	Graminoids	0.9/2	13.7/17	40.1/6
	Forbs	6.1/14	5.5/33	2.6/8
	Foliose lichens	0.1/1	0.4/10	1.0/7
	Fruticose lichens	0.5/1	11.8/20	0.9/28
	Crustose lichens	0.2/3	6.3/3	0.2/1
	Pleurocarpous mosses	25.6/6	8.3/21	33.5/12
	Acrocarpous mosses	9.0/10	7.4/34	10.3/12
	Liverworts	0.1/3	0.4/5	0.5/14
Soil properties	Physical properties			
	Moisture (vol.-%)	37.3 (2.6)	45.2 (2.5)	44.1 (1.3)
	Depth of O-horizon (cm)	0.4 (0.2)	15.3 (1.5)	11.9 (1.0)
	Bulk density (g/cm^3)	0.79 (0.03)	1.23 (0.07)	1.07 (0.04)
	Sand (%)	65.3 (2.3)	45.3 (2.7)	33.4 (1.9)
	Silt (%)	30.1 (2.6)	40.8 (3.0)	44.9 (1.1)
	Clay (%)	4.6 (0.8)	13.9 (1.2)	21.7 (1.8)
	Chemical properties			
	pH	7.9 (0.1)	7.9 (0.1)	5.3 (0.1)
	Total C (%)	6.30 (0.24)	5.78 (0.26)	3.46 (0.28)
	Total N (%)	0.18 (0.03)	0.29 (0.03)	0.21 (0.02)
	Ca (me/100g)	48.3 (1.8)	53.2 (2.7)	9.2 (0.5)
	Mg (me/100g)	1.78 (0.15)	1.86 (0.21)	1.59 (0.07)
	K (me/100g)	0.14 (0.02)	0.18 (0.02)	0.07 (0.01)
	Na (me/100g)	0.32 (0.14)	0.06 (0.01)	0.02 (0.01)
Cry. P.	Morphology	No pattern	No pattern	No pattern
	Thaw depth (cm)	65.0 (1.4)	64.9 (1.9)	33.6 (1.6)
	Frost heave (cm)**	3	3	3
	Needle-ice activity	None	None	None

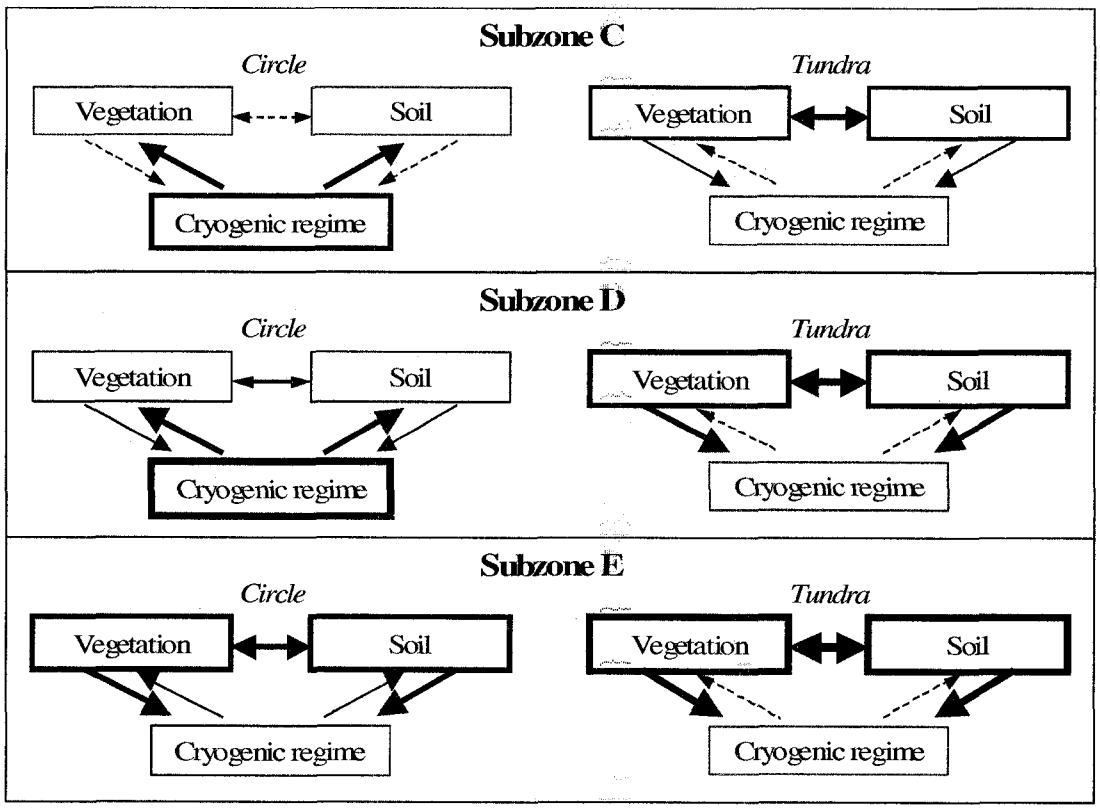

Fig. 5.1. Conceptual diagram of the interactions of the major components of the patterned-ground system (vegetation, soil and cryogenic regime as measured by frost heave, thaw depth and soil-surface stability) for nonsorted circles and the adjacent stable tundra along the bioclimate gradient. For each scenario, the line thickness of each box indicates the relative dominance the component has on the system. Bold arrows represent dominant interactions between the components, and dashed arrows are weak interactions. Diagram modified from Walker *et al.*, 2004.

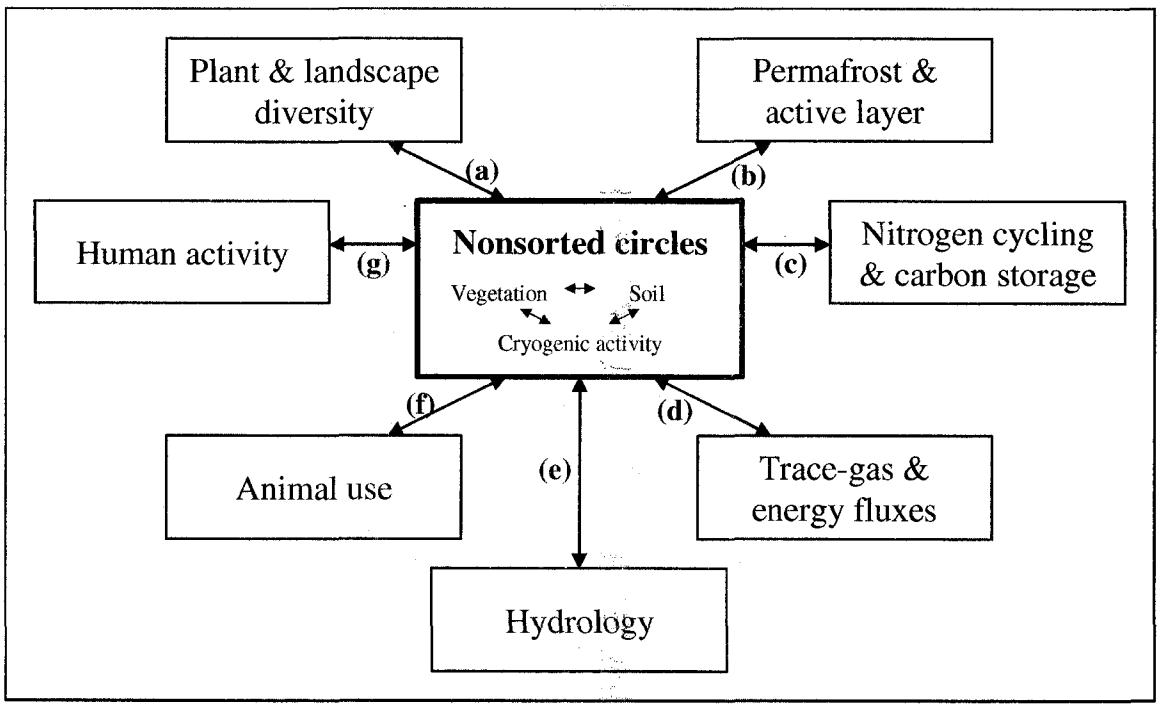

Fig. 5.2. The role of nonsorted circles on ecosystem dynamics. Nonsorted circles are linked to (a) plant and landscape diversity by increasing heterogeneity, (b) permafrost and active layer by increasing thaw depth, (c) nitrogen cycling through nitrogen fixation and carbon storage through cryoturbation of organic material, (d) decreased trace-gas and increased energy fluxes to the atmosphere, (e) water movement, (f) animal use through forage quality and habitat, and (g) human disturbance. See text for further explanation of the interactions. Diagram adapted from Walker *et al.*, 2004.

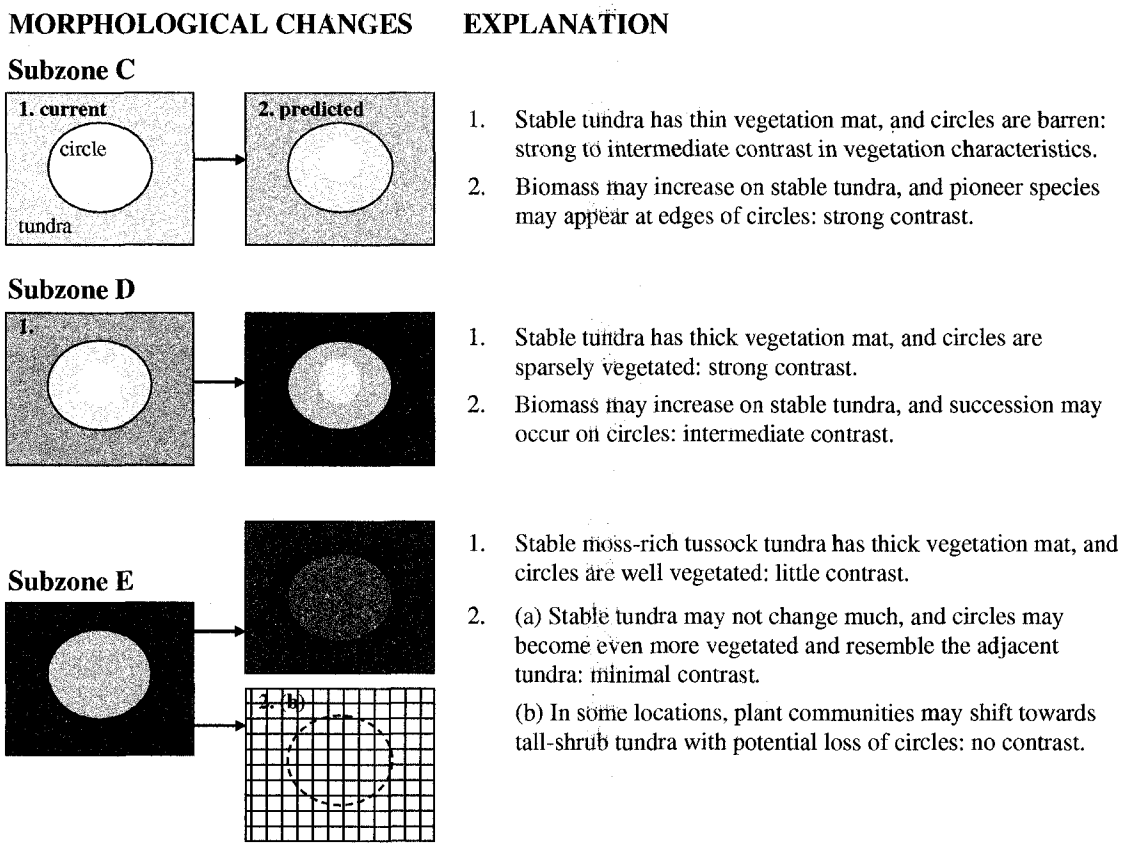

Fig. 5.3. Potential changes in the contrast of vegetation characteristics between nonsorted circles and the adjacent stable tundra along the bioclimate gradient under a warming arctic climate. The cartoons show possible morphological changes, with the amount of vegetation cover and biomass indicated by grey shading. The contrast in vegetation characteristics between nonsorted circles and the stable tundra is noted.

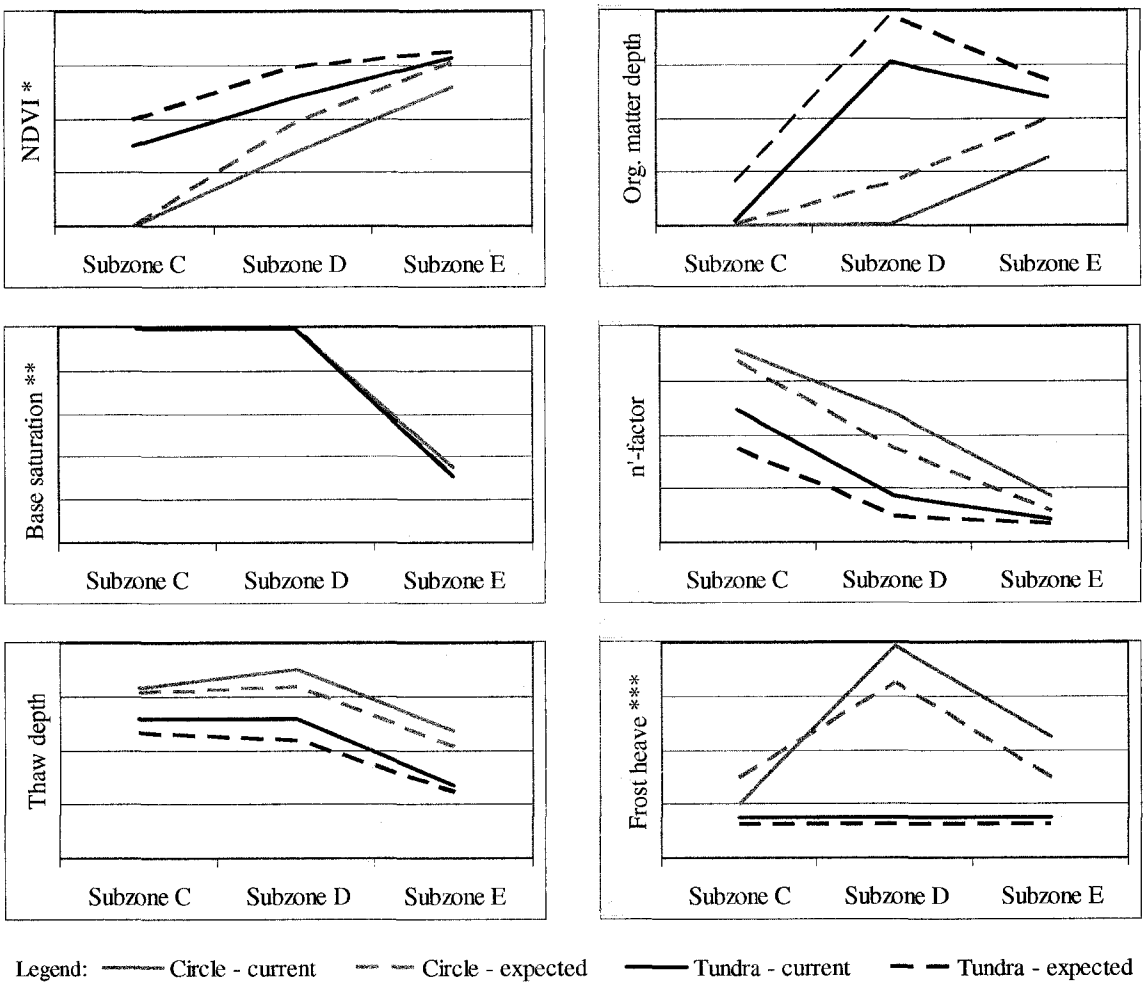

Fig. 5.4. Trends in current NDVI as a measure of biomass, depth of the soil organic layer, base saturation of the upper 10 cm of soil, n'-factor of the mineral soil, thaw depth and frost heave of nonsorted circles and the adjacent stable tundra along the bioclimate gradient and their conceptually anticipated change under a warming arctic climate. * Data from Kelley *et al.*, (2004). ** Data adapted from Michaelson *et al.*, (2005). *** Data from Walker *et al.*, (2004).